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GENETIC BEHAVIOR OF THE SPELT FORM IN CROSSES BETWEEN TRITICUM SPELTA AND TRITICUM SATIVUM [1]

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INTRODUCTION

In connection with genetic studies of density in the wheat spike, it was noted that the appearance of different specific forms in certain wheat crosses introduced marked irregularities in density curves of the second and following generations, and that the densities of *Triticum sativum* Lam., *T. polonicum* Linn., *T. spelta* Linn., etc., were affected in different degrees when a certain known density factor was introduced through hybridization. In some instances there were partial and sometimes total inhibitory effects in regard to density, depending upon the subspecies and also the kind of density factor involved in the cross.

The occurrence of these irregularities which appeared to be caused by the spelt character in some crosses led to the study of the nature and genetics of the species *T. spelta.* Although studies have been made of the mode of inheritance of the spelt form in a large number of interspecific crosses, only the different modes of inheritance in crosses where the parents are *spelta* and *sativum* are presented in this paper. In other crosses, such as *turgidum* Linn. × *sativum, durum* × *sativum, dicoccum* Schr. × *sativum,* etc., spelts invariably appear in the F_2 generation. The mode of inheritance of these spelt forms is complex and variable, so their discussion here has been omitted.

The plants on which these studies were made were grown, with a few exceptions, on Arlington Farm, near Washington, D. C., or on the Plant Introduction Station, Chico, Calif., both operated by the United States Department of Agriculture. The crosses were made at the former place in 1913.

[1] The specific name *T. sativum* as used in this paper refers only to the forms *T. vulgare* Vill., *T. compactum* Host., and *T. capitatum* Schlz. These three forms are essentially the same species, their differences being merely a question of internode length. The word wheat is frequently used as an English designation for these forms, and when so used does not include such other forms as *T. durum* Desf., *T. polonicum,* etc.

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SPECIFIC DIFFERENCES BETWEEN TRITICUM SATIVUM AND TRITICUM SPELTA

The shape of the outer or sterile glume is an important character in the differentiation of wheat species. The glume of the true *T. sativum* form (fig. 1, B) is, as a rule, soft, with a somewhat pointed apex. It is rarely and very weakly keeled along the entire length. About 0.5 to 1 mm.

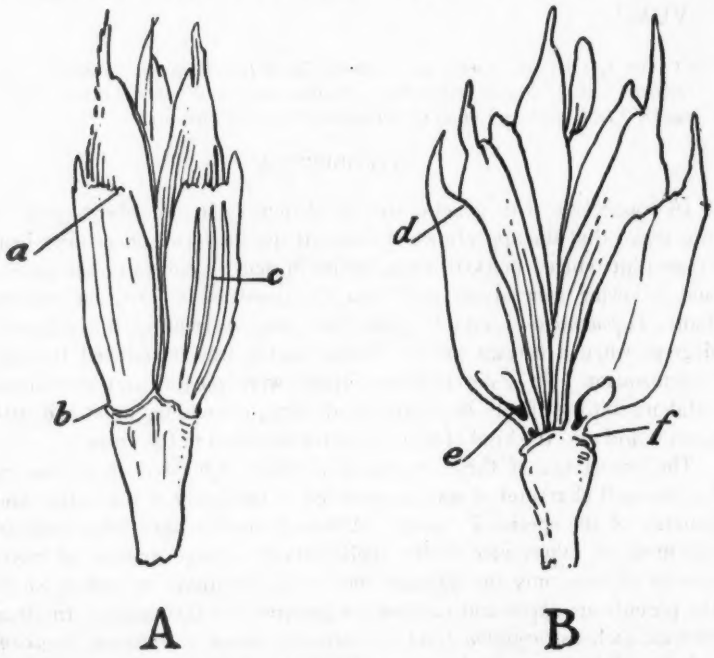

FIG. 1.—Characteristic spikelets of *Triticum spelta* (A) and *Triticum sativum* (B). Note upright and tight position of the glumes of *spelta* and the loose, spreading habit of *sativum*. *Spelta* has a flat shoulder (*a*) with two or three indentations; the shoulder of *sativum* (*d*), though varying widely, is generally not so prominent. It is often rather tapering with no indentations. The base of the sterile glume of *spelta* (*b*) is broad, showing firm attachment to the rachis. The glumes can not be opened without breaking them at the base. In *sativum* the base (*f*) is narrow and is weakly attached to the rachis, and the glumes can be opened easily. There are one or more depressions (*e*) at the base of the glume in *sativum* which are not present in *spelta*. The glume of *spelta* is more or less uniform in width. It is stiff and has prominent corrugations (*c*); that of *sativum* is narrow at base, widens, then tapers again gradually. It is very thin and soft, and the veins on the glumes are not so prominent. *Sativum* has a weak keel while *spelta* has a very strong one. The *Spelta* spikelet usually develops only two kernels; *sativum* often develops three or more.

above the point of attachment there is a wrinkle or depression. The base is rather narrow and is very weakly attached to the rachis. The glume characters of the typical spelt, on the other hand, are quite different (fig. 1, A). The glume is stiff and thick, with a very blunt apex. It is strongly keeled and has no depression above the base, which is wide and firmly attached to the rachis.

Some wheats exhibit some of the spelt characters in a very weak form. For instance, some are more or less strongly keeled or have a flat shoulder at the distal part of the glume. While such wheats are classified as *T. sativum*, they are not true *sativum* in the sense used here. They do not represent the type.

Aside from the glumes, these species have other distinguishing characters. Of these, the brittleness of the rachis and nonshattering qualities of the spikelet in spelt may be mentioned as contrasted with the *sativum* types, the latter being nonbrittle and shattering easily.

Although the heads of the spelt varieties commonly grown at experiment stations in this country usually are lax, laxness of the head is not necessarily a characteristic of the spelt. Compactness may easily be introduced into spelts when crossed with *T. compactum*, which is really only a wheat carrying a genetic factor or factors for compactness.

The characters differentiating these two species are recapitulated below. This list includes also some other minor characters.

T. sativum.	*T. spelta.*
Outer glumes—	Outer glumes—
Weakly attached by narrow base.	Firmly attached by wide base.
Weakly keeled.	Strongly keeled.
Apex tapering.	Apex blunt.
Depression or wrinkle near point of attachment.	No wrinkle near base.
Veins not prominent.	Prominent parallel longitudinal veins.
Shoulder narrow to broad, with no dentation.	Shoulder broad, with two or three dentations.
Glume soft.	Glume, lemma, and palea firm and thick.
Spikelets—	Spikelets—
Kernel loosely held between glumes (shattering).	Kernel tightly held (nonshattering).
Spikelets spreading somewhat from rachis.	Spikelets oppressed tightly against the rachis.
Usually three or more kernels per spikelet.	Usually two and rarely three kernels per spikelet.
Rachis—	Rachis—
Tenacious.	Fragile.

There also are differences in the shape of the kernels of these two species (*1*).[1]

LINKAGE OF SPECIFIC CHARACTERS

In order to understand the manner in which these two forms are here classified, it is necessary to refer to the linkage of their specific characters, without discussing the details.

Most of the characters tabulated above show two limits of contrasts. When a wheat is crossed with a spelt, a gradation of forms naturally

[1] Reference is made by number (italic) to "Literature cited," p. 363-364.

appears in the F_2 generation, ranging from the true spelt to the typical wheat form. In the segregates, a plant which has the glume form of the spelt invariably has a brittle rachis and a nonshattering habit. If the glume form is intermediate, the brittleness and shattering qualities also are intermediate. These three characters do not segregate independently. A plant with *sativum* glumes, for instance, has not been found whose rachis is brittle (a characteristic of the spelt only), nor have we obtained a spelt-glumed plant which has as tenacious a rachis as that of *T. sativum*. These species may present other characters, such as pubescence, beardedness, glume color, etc. These are common to both and segregate independently irrespective of the species. The presence of correlation between some of these specific characters in *sativum* × *spelta* crosses also has been noted by von Tschermak (*12*).

Unless the linkage is absolute it does not exclude the possibility of the occurrence of crossovers, but if crossing over ever occurs with respect to these characters it must be very rare.

The linkage of specific characters of spelt is very similar to the linkage of a number of glume characters of the wild oats in crosses between wild and cultivated forms described by Surface (*11*) and by Love and Craig (5).

It is absolutely necessary to bear in mind that the determination of the species is based only upon the presence, intensity of development, or absence of the specific characters (glume characters, brittleness of rachis, and seed-holding habit), all of which are linked to a very large extent. These characters show no independent segregation. It is obvious, therefore, that they do not mendelize independently. The characters which do segregate independently, such as pubescence, beardedness, glume color, etc., are not taken into consideration.[1]

METHOD OF CLASSIFYING THE FORMS

The second and subsequent filial generations of *spelta* × *sativum* crosses show numerous gradations between the two parental forms. Some of the F_2 plants produced a progeny consisting of individuals which were decidedly spelts, while others produced a progeny which, while all spelts, yet resembled *T. sativum* to some extent and were distinctly different from the former group of plants where all the individuals were markedly spelt-like.

Ten arbitrary classes were made in order to record the degree of inheritance of spelt characters. The typical or intense spelt which exhibited all the specific spelt characters in their extreme forms was graded 1. As the exhibition of the intensity of these characters diminished—that is, as they tended to approach those of the wheat—the heads were

[1] Even these independently segregating characters vary in intensity and quality in these two species when segregating in crosses.

classed 2, 3, and so on to 9. Class 10 includes only true wheats, the forms which show absolutely no trace of the spelt characters. It must be emphasized that these 10 classes are purely arbitrary, based upon the appearances of the heads, and are not intended to represent any genotypic classes. The types representing these 10 classes are presented in Plate 33, A.

When the degree of inheritance of the spelt characters by a heterozygous population is recorded on two different occasions, a variation in the class frequencies naturally may be expected, but the general form of the curve remains practically the same. The error which may affect the conclusions rests in the decision as to whether a particular plant belongs to class 9 or 10. The degree of error depends upon the cross examined.

Of the plants discussed herein, which were tested in the F_3 generation, there were five cases where individuals belonging in class 9 had been placed in class 10 and only one case where a class 10 individual was erroneously recorded as belonging to class 9. In the tables these six corrections have been made. As the conclusions are based not merely on the F_2 individuals but upon the progeny of these, it does not seem likely that this source of error could have affected the results to any extent.

The spelt parents used for making the crosses graded from 1 to 4; the variety of wheat known as Gatineau [1] and herein considered as speltoid in form graded from 4 to 7; and all the *T. sativum* parents of course graded 10. As the discussions in this paper are confined only to the spelt character it does not seem necessary to describe further the agronomic and botanical characteristics of the plants used in making the crosses, as these have no direct bearing on the subject.

FAMILIES SHOWING THE PRESENCE OF ONLY ONE FACTOR FOR SPELTING [2]

The hybrids of the first filial generation (F_1) of a *spelta* × *sativum* cross are slightly intermediate in form, resembling the spelt more than the *sativum* parent. They grade from 4 to 7, depending upon the cross. They possess all the characteristics of a spelt, but the spikelets may be somewhat more open and the grains may not be so firmly held within the glumes. The spelt characters are so nearly completely dominant that they inhibit all wheat characters.

In the second generation a segregation is obtained where the individuals vary, producing forms ranging from the typical wheat form to

[1] This variety originated as a cross of Red Fife ♀ (*T. sativum*) and Goose ♂ (*T. durum*) (*10, p. 239*). It is a striking illustration of the spelt-like segregates which appear when these two wheat species are crossed. The heads are so much like spelt that at blooming time especially it is easily mistaken for spelt, but it thrashes free and is otherwise like the common wheats.

[2] For brevity, "spelting" is used throughout this paper in place of "inheritance of the spelt characters."

the spelt. The curve of these gradations is not a binomial frequency curve, but, on the contrary, more individuals are found, as a rule, at the extremities of the range than near the center. This fact may be observed in Table I, which shows the forms of the F_2 segregates.

TABLE I.—*Number of plants of the F_2 generation falling into each of 10 classes, based on presence or absence of spelt characters, with total number of spelts and wheats actually obtained, calculated numbers on basis of 3 to 1 ratio, deviation, probable error, and ratio between deviation and probable error*

Series.	Crosses.	Number falling in class—										Total.
		1	2	3	4	5	6	7	8	9	10	
13255a	Spelt sel. 13440×Dale Gloria sel. 13401	17	10	9	5	4	1	3	1	2	21	73
13260a	Spelt sel. 13438×Turkey (C. I. 3375) sel. 13389	17	13	5	5	2	3	2	...	2	14	63
13263a	Dale Gloria sel. 13401×spelt	5	3	2	3	1	...	2	2	...	7	25
3094a	Black Bearded spelt×Early Red Chief	19	7	5	...	3	4	3	5	6	29	81
3085a	Black Bearded spelt×Jones Longberry	9	8	4	2	4	...	4	2	4	13	50
13124a	Vulgare (C. I. 3338)×spelt sel. 13437	9	8	4	9	7	4	3	5	7	20	76
13125a	Crimean (C. I. 3340) sel. 13351×spelt sel. 13437	6	3	9	3	4	2	5	5	4	9	50
	Total of crosses											418

Series.	Crosses.	Number of plants.				Deviation.	Probable error.	Ratio $\frac{\text{Dev.}}{\text{P. E.}}$
		Obtained.		Calculated.				
		Spelts.	Wheats.	Spelts.	Wheats.			
13255a	Spelt sel. 13440×Dale Gloria sel. 13401	52	21	54.8	18.2	2.8	2.5	1.12
13260a	Spelt sel. 13438×Turkey (C. I. 3375) sel. 13389	49	14	47.3	15.7	1.7	2.3	.74
13263a	Dale Gloria sel. 13401×spelt	18	7	18.8	6.2	.8	1.4	.57
3049a	Black Bearded spelt×Early Red Chief	52	29	60.8	20.3	8.8	2.6	3.38
3085a	Black Bearded spelt×Jones Longberry	37	13	37.5	12.5	.5	2.1	.24
13124a	Vulgare (C. I. 3338)×spelt sel. 13437	56	20	57.0	19.0	1.0	2.5	.40
13125a	Crimean (C. I. 3340) sel. 13351×spelt sel. 13437	41	9	37.5	12.5	3.5	2.1	1.67
	Total of crosses	305	113	313.5	104.5	8.5	6.0	1.42

As it is impossible to distinguish the homozygous spelts from the heterozygous forms, in determining the ratios all the spelt and speltoid forms (classes 1 to 9) have been grouped together and compared with

the wheat forms (class 10), which show no trace of spelt characters. The proportions between *spelta* and *sativum* forms of each of the crosses taken separately and that of the totals of these two groups approximated the monohybrid ratio of 3 to 1. The obtained ratio of the totals of the crosses was 305 speltoid and spelt forms to 113 wheats, the expections being 313.5 to 104.5, respectively, showing a deviation of 8.5 with a probable error of ± 6.0.

Two of the F_2 families, 13260a and 13255a, gave the results shown in Table II when the F_3 generation was grown.

Table II shows that the F_2 population of the families tested consisted of individuals in the proportion of 1 homozygous spelt to 2 heterozygous forms and 1 homozygous wheat.

TABLE II.—*Number of F_2 plants from series 13260a and 13255a which proved to be homozygous spelts, heterozygous forms, and homozygous wheats (1 : 2 : 1) when tested in the F_3 generation*

Nature of data.	13260a, Spelt × Turkey.				13255a, Dale Gloria × Turkey.			
	Homozygous spelts.	Heterozygous forms.	Homozygous wheats.	Total.	Homozygous spelts.	Heterozygous forms.	Homozygous wheats.	Total.
Obtained.....	8	13	9	30	7	14	12	33
Calculated.....	7.5	15.0	7.5	.....	8.2	16.5	8.2	.....
Deviation.....	.5	2.0	.5	.....	1.2	2.5	3.8	.....

The ratios of the totals of the forms produced in the F_3 generation by the heterozygous F_2 individuals of these two families (Table III) seem to conform to the foregoing assumption, although the ratios of the forms produced by each of the F_2 individuals sometimes are not so close to the 3 to 1 expectation. Of the total individuals produced by the F_2 heterozygous plants of series 13260a (spelt × Turkey), 212 were spelts and 71 wheats. These results were surprisingly close to the expectation, the deviation from the calculated numbers being but 0.3 with a probable error of ±4.9. In series 13255a (Dale Gloria × spelt), the numbers obtained from the heterozygous individuals were 365 spelts and speltoids and 156 wheats; the deviation here was 25.8 with a probable error of ±6.7. This apparent dominance of the spelt character over that of the wheat and its segregation into the 3 to 1 ratio are in accord with the observations of Pitsch, as cited by von Tschermak (*12, p. 179*) and of Kajanus (*3*).

TABLE III.—*Numbers of spelts and wheats produced in the F_3 generation from the F_2 heterozygous plants, and comparison of these with theoretical expectations, calculated on the 3 to 1 basis*

Pedigree No.	Total F_2 plants.	Number of plants.				Deviation.	Probable error.	Ratio Dev. / P. E.
		Obtained.		Calculated.				
		Spelts.	Wheats.	Spelts.	Wheats.			
13260a–3....	23	13	10	17.3	5.7	4.3	1.4	3.1
6....	20	16	4	15.0	5.0	1.0	1.3	.8
7....	28	20	8	21.0	7.0	1.0	1.5	.7
9....	17	10	7	12.8	4.2	2.8	1.2	2.3
10...	23	18	5	17.3	5.7	.7	1.4	.5
13...	24	17	7	18.0	6.0	1.0	1.4	.7
14...	17	13	4	12.8	4.2	.2	1.2	.2
15...	20	16	4	15.0	5.0	1.0	1.3	.8
19...	29	26	3	21.8	7.2	4.2	1.6	2.6
25...	17	13	4	12.8	4.2	.2	1.2	.2
28...	17	12	5	12.8	4.2	.8	1.2	.7
29...	18	16	2	13.5	4.5	2.5	1.2	2.1
30...	30	22	8	22.5	7.5	.5	1.6	.3
Total..	283	212	71	212.3	70.7	.3	4.9	.1
13255a–7....	36	34	2	27.0	9.0	7.0	1.7	4.1
8....	19	15	4	14.3	4.7	.7	1.3	.5
10...	24	20	4	18.0	6.0	2.0	1.4	1.4
11 ..	35	27	8	26.3	8.7	.7	1.7	4.1
15...	59	44	15	44.3	14.7	.3	2.2	.1
16...	33	23	10	24.8	8.2	1.8	1.7	1.1
17...	13	4	9	9.8	3.2	5.8	1.0	5.8
21...	52	28	24	39.0	13.0	11.0	2.1	5.2
23...	49	29	20	36.8	12.2	7.8	2.0	3.9
24...	35	18	17	26.3	8.7	8.3	1.7	4.9
25...	44	33	11	33.0	11.0	0	.....	.....
26...	37	25	12	27.8	9.2	2.8	1.8	1.6
28...	50	33	17	37.5	12.5	4.5	2.1	2.1
30...	35	32	3	26.3	8.7	5.7	1.7	3.4
Total..	521	365	156	390.8	130.2	25.8	6.7	3.9

FAMILIES SHOWING THE PRESENCE OF TWO SPELT FACTORS

Of the crosses studied, two families, 13126a (Giant Squarehead × spelt) and 3019a (spelt × Salt Lake Club) produced a very low proportion of wheat types. Not much importance would have been attached to the irregular behavior of these families if an apparently similar behavior had not been observed in another *sativum* × *spelta* cross. The manner of segregation of the progeny of these two crosses is given in Table IV.

TABLE IV.—*Degree of spelting and proportions of spelts and wheats obtained in the F_2 generations of spelta × sativum crosses which did not segregate in the 3 to 1 ratio*

Series.	Degree of spelting in class—										Total.	Number of plants.				Deviation.	Probable error.
	1	2	3	4	5	6	7	8	9	10		Obtained.		Calculated.			
												Spelt.	Wheat.	Spelt.	Wheat.		
13126a [1]....	12	7	7	6	9	8	3	6	12	4	74	70	4	69.4	4.6	0.6	1.40
3019a [2].....	27	15	9	7	3	5	2	5	8	2	83	81	2	77.8	5.2	3.2	1.49

[1] Series 13126a, Giant Squarehead (C. I. No. 3351, selection 13366) × spelt (selection 13437).
[2] Series 3019a, white spelt × Salt Lake Club.

In series 13126a (Table IV), only 4 wheats were produced in a population of 74 F_2 plants, while in series 3019a, 2 wheats were produced in an F_2 population of 83 individuals. The deviation from the 3 to 1 ratio is so great that even by grouping class 9 with class 10—that is, by making generous allowances for observational error—the proportion approached more nearly the 15 to 1 ratio. On the basis of the 15 to 1 ratio, the expectation in series 13126a, is 69.4 to 4.6, in series 3019a, 77.8 to 5.2. The deviations are 0.6 and 3.2, and the probable errors ± 1.40 and ± 1.49, respectively.

On examining the F_3 generation produced from 27 plants of series 13126a, it was found that 12 of these had produced only spelts (Table V), two plants yielded only *sativum* types, and the remaining 13 F_2 plants yielded progeny of mixed forms. Assuming that the spelt parent in this particular cross carried two spelt factors, S_1 and S_2,[1] the first two generations will consist of the following genotypic forms:

P_1	(Giant Squarehead) *T. sativum*	$s_1s_1s_2s_2 \times S_1S_1S_2S_2$		(Winter spelt) *T. spelta*
F_1		$S_1s_1S_2s_2$ (Speltoid)		
F_2	1 $s_1s_1s_2s_2$	1 $S_1S_1S_2S_2$ 2 $S_1S_1S_2s_2$ 1 $S_1S_1s_2s_2$ 2 $S_1s_1S_2S_2$ 1 $s_1s_1S_2S_2$	4 $S_1s_1S_2s_2$	2 $S_1s_1s_2s_2$ 2 $s_1s_1S_2s_2$
Total	1 *T. sativum*.	15 spelts.		

If these genotypes were carried through the F_3 generation the theoretical behavior of each of the F_2 plants would be as follows:

GROUPS.	F_2 GENOTYPES.	PHENOTYPES OF THE F_2 AND THEIR BEHAVIOR IN THE F_3 GENERATION.	
A.....	1 $s_1s_1s_2s_2$	1 wheat will yield wheat only.	
B.....	1 $S_1S_1S_2S_2$	7 spelts will yield spelts only.	
	2 $S_1S_1S_2s_2$		
	1 $S_1S_1s_2s_2$		
	2 $S_1s_1S_2S_2$		
	1 $s_1s_1S_2S_2$		
C.....	4 $S_1s_1S_2s_2$	4 spelts will segregate 15:1	8 unstable forms.
D.....	2 $S_1s_1s_2s_2$	4 spelts will segregate 3:1	
	2 $s_1s_1S_2s_2$		
Total.....		16	

When the performances of the F_2 plants were examined, a close approximation was found to the above-mentioned theoretical ratios. The numbers of constant wheats, constant spelts, and unstable spelt forms obtained are shown in Table V, together with the theoretical expectations.

[1] In the factorial explanations given in this paper the spelt factors are assumed to be S_1 and S_2. Although the assumption of the factors s_1 and s_2 to stand for the wheat (*T. sativum*) character will fully agree with the results obtained, so far as the ratios go, there is no evidence as yet to warrant the assumption that the wheat and spelt characters are allelomorphic to each other. In fact, results with other specific crosses show the possibility that these are caused by two sets of independent factors. The behavior of the *sativum* × *spelta* crosses may be compared with the behavior of a maize cross where one parent has yellow endosperm and purple aleurone color (YYCCPP), and the other differs from this by its lack of purple color (YYCCpp). In such a cross, where the F_2 shows segregation into 3 purple to 1 yellow, the assumption that yellow and purple are allelomorphic may be used as a working hypothesis for crosses of this type, although it is not the correct explanation, as endosperm and aleurone color are two different characters altogether.

TABLE V.—*Frequencies of spelt and wheat classes in F_3 progeny of F_2 individuals of family 13126a, Giant Squarehead × spelt*

FAMILIES CONSISTING OF WHEATS ONLY

Pedigree numbers of F_2	Class of F_2 parent plant.	Classes of spelt inheritance F_3— 1	2	3	4	5	6	7	8	9	10	Number of plants. Spelts and speltoids.	Wheats.	Total.
3	10	..	..	..	..	..	..	..	..	..	4	.....	4	4
23	10	..	..	..	..	..	..	..	..	..	10	.....	10	10

FAMILIES CONSISTING OF SPELTS ONLY

2	5	6	6	4	1	1	..	..	..	..	..	18	.....	18
4	3	5	4	1	..	..	..	..	..	..	..	10	.....	10
5	9	..	..	..	..	..	..	..	..	13	..	13	.....	13
7	7	..	2	6	1	2	..	1	1	..	..	13	.....	13
8	3	9	2	1	1	..	..	..	..	..	..	13	.....	13
12	6	..	1	2	..	..	..	..	..	2	..	5	.....	5
15	4	4	2	3	2	2	1	..	1	3	..	18	.....	18
16	5	3	1	3	1	2	1	..	1	2	..	14	.....	14
20	6	1	..	1	1	..	..	..	..	..	..	5	.....	5
22	.....	2	3	2	3	1	1	1	..	1	..	14	.....	14
24	1	3	4	2	..	1	..	..	..	..	..	10	.....	10
25	.....	..	..	..	..	..	1	3	..	1	..	5	.....	5
Total	.....	..	..	..	..	..	..	..	..	..	..	138	.....	138

FAMILIES CONSISTING OF SPELTS AND WHEATS (HETEROZYGOUS F_2 PLANTS)

1	5	1	2	5	3	1	1	1	1	1	1	16	1	17
6	6	..	3	1	1	1	..	..	2	1	2	9	2	11
9	8	..	2	..	..	..	..	1	1	1	2	5	2	7
10	9	..	..	..	..	..	..	..	..	3	1	3	1	4
11	8	..	1	..	1	1	1	1	1	1	1	7	1	8
13	8	..	..	..	..	..	..	..	1	13	1	14	1	15
14	7	2	3	1	..	1	..	..	..	..	4	7	4	11
17	5	2	5	3	1	..	..	..	..	3	1	14	1	15
18	8	1	2	4	2	2	1	..	1	3	1	16	1	17
19	1	1	3	..	..	1	..	..	..	..	1	5	1	6
21	1	2	5	5	2	1	1	..	..	2	4	18	4	22
26	9	..	..	..	..	..	..	1	..	3	2	4	2	6
27	5	..	1	1	..	1	..	..	1	1	1	5	1	6
Total progeny of heterozygous F_2 plants	.....	..	..	..	..	..	..	..	..	..	..	123	22	145
Expectations	.....	..	..	..	..	..	..	..	..	..	..	108.75	36.25	.....

SUMMARY AND GROUPING

Groups.	Types.	Number of plants. Obtained.	Calculated 7:8:1.	Deviation.
A	Wheats producing wheats only	2	1.7	0.3
B	Spelts producing only spelts	12	11.8	.2
C and D	Spelts producing both spelts and wheats	13	13.5	.5

The agreement between the proportions expected and those obtained is very close indeed to the 7 to 8 to 1 ratio, and perhaps too close to be ordinarily expected from such a small population.

The analysis may be carried a step further. As shown above, the plants which would show unstability in the F_3 (groups C and D), were expected to be of two different genotypes. One of them, containing the $S_1s_1S_2s_2$ forms (group C), was expected to segregate in the 15 to 1 ratio, while the other (group D), containing the $S_1s_1s_2s_2$ and $s_1s_1S_2s_2$ genotypes, should segregate in the simple 3 to 1 monohybrid ratio. Apparently the individuals belonging to each of these two groups are those analyzed in Table VI.

TABLE VI.—*Analyses of unstable spelts of the F_2 generation, series 13126a. Number of individuals of the F_3 generation produced from F_2 plants of groups C and D, compared with the theoretical expectation*

F_2 INDIVIDUALS APPARENTLY SEGREGATING IN THE 15 TO 1 RATIO (GROUP C, $S_1s_1S_2s_2$)

Pedigree.	Total.	Number of plants.				Deviation.	Probable error.	Ratio Dev. / P. E.
		F_3 obtained.		F_3 calculated.				
		Spelts.	Wheats.	Spelts.	Wheats.			
13126a–1....	17	16	1	15.9	1.1	0.1	0.68	0.1
11...	8	7	1	7.5	.5	.5	.46	1.1
13...	15	14	1	14.1	.9	.1	.62	.1
17...	15	14	1	14.1	.9	.1	.62	.1
18...	17	16	1	15.9	1.1	.1	.68	.1
Total..	72	67	5	67.5	4.5	.5	1.38	.3

F_2 INDIVIDUALS APPARENTLY SEGREGATING IN THE 3 TO 1 RATIO (GROUP D, $S_1s_1s_2s_2$ AND $s_1s_1S_2s_2$)

13126a–6....	11	9	2	8.3	2.7	0.7	0.96	0.7
9....	7	5	2	5.3	1.7	.3	.77	.4
10...	4	3	1	3.0	1.0	0	.....	.....
14...	11	7	4	8.3	2.7	1.3	.96	1.4
19...	6	5	1	4.5	1.5	.5	.72	.7
21...	22	18	4	16.5	5.5	1.5	1.37	.1
26...	6	4	2	4.5	1.5	.5	.72	.7
27...	6	5	1	4.5	1.5	.5	.72	.7
Total..	73	56	17	54.8	18.2	1.2	2.50	.5

Total F_3 plants segregating in 15 to 1 ratio, obtained, 5.
Total F_3 plants segregating in 15 to 1 ratio, calculated, 6.7.
Deviation, 1.7.
Total F_3 plants segregating in 3 to 1 ratio, obtained, 8.
Total F_3 plants segregating in 3 to 1 ratio, calculated, 6.7.
Deviation, 1.3.

The data in Table VI show that forms were obtained in the F_2 some of which segregated in the 15 to 1 and others in the 3 to 1 ratio as expected. The agreement to the theoretical numbers of the progeny of each F_2 plant is as close as can be expected with such small numbers, even

though it is borne in mind that the values of the probable error are likely to be too high in data of this kind.

Summing up the types of groups C and D, the former yielded 67 spelts to 5 wheats, and the latter group yielded 56 spelts to 17 wheats, the deviation being 0.5 and 1.2 and the probable errors ± 1.38 and ± 2.50, respectively.

Of the 27 plants tested (Tables V and VI), 5 (group C) showed an approximation to the 15 to 1 ratio and 8 (group D) to the 3 to 1 ratio. The theoretical number of plants belonging to each of the two unstable groups was 6.7—that is, one-fourth of the total F_2 plants tested. Comparing the results obtained with those expected, it will be noted that there were in the F_2 generation two (1.7 actual) $S_1s_1S_2s_2$ individuals less and one (1.3 actual) $S_1s_1s_2s_2$ or $s_1s_1S_2s_2$ more than expected (Table VI).

In considering the 15 spelt to 1 wheat segregation, it should be borne in mind that if the progeny of a heterozygous F_2 plant is less than about 10 individuals, the chances are that the wheat form, which is expected to appear but once in a population of 16 individuals, will not be obtained. Such heterozygous plants producing only spelts and no wheats, on account of their small F_3 population, would be classified under group B. Had F_2 plants 13126a − 12, − 20, and − 25 produced more than 4 or 5 individuals, 1 or 2 of them might have produced a wheat form which would have placed them in group C. The experimental ratios then would almost coincide with the theoretical.

Considering the closeness of agreement even in the details of the analysis, with such small numbers, there seems to be no question that we are dealing here with two spelt factors and that the ratio observed is the ratio of 15 to 1.

In the absence of more experimental evidence, the simplest hypotheses were given to account for the 3 to 1 and 15 to 1 segregations. Notwithstanding the surprisingly close agreements between the experimental and theoretical ratios, however, the real explanation concerning the production of the spelt character is still a matter of speculation.

The same spelt parent plant was used in crosses 13124a, 13125a, and 13126a. The wheat parents were of different varieties. No satisfactory explanation can be offered as to why the same spelt parent should produce a 15 to 1 ratio in cross 13126a and a ratio of 3 to 1 in crosses 13124a and 13125a. Three possibilities, however, may be mentioned.

1. The spelt plant used in the above-mentioned three crosses might have been heterozygous for one of the spelt factors. Such a heterozygous $S_1s_1S_2S_2$ plant bears gametes producing 3 to 1 and 15 to 1 ratios in the F_2 generation when crossed with a double recessive ($s_1s_1s_2s_2$) wheat.

2. The spelt parent may be assumed to have carried two spelt factors S_1 and S_2 and some of the wheats might have carried an inhibiting factor I. If the wheat carried the I factor the ratio of spelt to nonspelt would be about 3 to 1 and if it did not the ratio would be 15 to 1.

3. The spelt might have carried a spelt factor S_1 and in addition another factor S_2, which would produce the spelt character if there were present its complementary factor C, which might have been supplied by the wheat parent. In this case if C were present the ratio would be about 8 spelts to 1 wheat; and if C were not present, it would be 3 to 1. The ratios to be expected on the basis of this last possibility, however, are not in accord with the experimental results.

The second explanation seems to be the most plausible of the three. The assumption that some wheats carry the factor for the inhibition of the spelt character is not a mere speculation but a fact, as will be seen later when the question of the production of synthetic spelts by crossing two wheats is taken up. As commercial strains of *T. sativum* are not purified with respect to inhibitors, there are undoubtedly some strains which contain individuals heterozygous for this factor. If such a plant is used, for instance, as the female parent and is crossed with a spelt carrying the factor for spelting, according to the hypothesis some of the seeds will produce F_2 progeny where in some instances the ratio will suggest a 15 to 1, and in others a 3 to 1 segregation. As will be seen later, other modifications of these ratios may also be expected to arise.

PROGENY OF STABILIZED SPELTOID × SATIVUM CROSSES

The speltoid form used in the crosses which will be considered now is commercially known as "Gatineau." The variety originated from a cross between *T. durum* and *T. sativum*. It grades usually from 4 to 7 in the classification used in this study for spike form and so resembles the commercial spelts in this respect. It does not have the brittle rachis of spelt, and the grain thrashes from the glumes more easily than the grain of spelt, being like some of the tight-glumed wheats. It is neither a typical *spelta* nor a typical *sativum*.

The F_1 plants of the crosses between Gatineau and *T. sativum* were almost like Gatineau. The F_2 generation consisted of forms which were intermediate; typical spelts of classes 1 to 2 were not found. The classification of the F_2 individuals is reproduced in Table VII.

TABLE VII.—*Classes of F_2 generation plants of two speltoid × wheat crosses. Numbers of individuals obtained compared with the theoretical expectations*

Series.	Degree of spelting.											Number of plants.				Deviation.	Probable error.
												Obtained.		Calculated.			
	1	2	3	4	5	6	7	8	9	10	Total.	Speltoid.	Wheat	Speltoid.	Wheat		
13228a [1]	0	0	2	2	4	9	10	11	15	15	68	53	15	51.0	17.0	2.0	2.4
13229a [2]	0	0	1	0	5	9	7	9	15	17	63	46	17	47.2	15.8	1.2	2.3

[1] Series 13228a Turkey (C. I. 3375, Sel. 13389) × Gatineau (C. I. 2959, Sel. 13403).
[2] Series 13229a Seneca Chief (C. I. 3372, Sel. 13388) × Gatineau (C. I. 2959, Sel. 13403).

So far as the ratios of speltoid to wheat forms are concerned, these crosses segregated in the simple mendelian fashion. In series 13228a (Turkey × Gatineau) there were 53 speltoids and 15 wheats, showing a deviation from the theoretical numbers of 2.0 with a probable error of ±2.4 In series 13229a (Seneca Chief × Gatineau) there were 46 speltoids and 17 wheats, the deviation here being 1.2 with a probable error of ±2.3. In both cases the approximations of the figures obtained to those expected are within the range of their probable erros. Therefore, it can safely be concluded that the ratio is 3 to 1 and that there very likely is but one spelt factor difference.

The question of interest in the inheritance of this speltoid form (Gatineau) is not so much in its 3 to 1 ratio as in the way it differs in details from the spelt × wheat crosses first discussed, which segregated in the ratio of 3 to 1.

In order to compare the F_2 curves of these two groups of spelt × wheat crosses, the F_2 frequencies in Table VII (series 13228a and 13229a) and the first two series in Table I (13255a and 13260a) are represented graphically (fig. 2).

The comparative characteristics of the curves of these two sets of crosses are as follows:

The curves of the true spelt × wheat crosses (13255a and 13260a) begin at class 1, where they have their highest spelt frequencies. They gradually drop until they reach classes 5 to 9, inclusive, where there seems to be an indefinite fluctuation of frequencies. Then the curves suddenly rise again at class 10, which contains the spelt-free populations.

As to the curves of the wheat × speltoid crosses, the F_2 spelt populations begin at about class 3, where but a very few individuals are found. Beginning at class 5, the curves steadily rise until they reach their maximum height at class 10. The curves produced by the true spelt crosses, it will be recalled, continuously dropped instead of ascending.

When these two sets of crosses are compared it will be observed that, although there is but one spelt factor difference in each, the spelt factor present in crosses 13255a and 13260a is entirely different from the spelt factor present in crosses 13228a and 13229a. The wheat parent has had no influence is producing this variation in distribution, the same wheat parent plant, Turkey, C. I. No. 3375, selection 13389, having been used in crosses 13260a and 13228a.

GENERAL DISCUSSION OF THE GROUPINGS WITHIN THE SPELT AND SPELTOID CLASSES

Having discussed the question of ratios, let us turn our attention to the analyses of the details of the variations within the spelt and speltoid classes.

The possibility of distinguishing the homozygous from the heterozygous spelts of the F_2 generation is of primary interest. Table VIII has

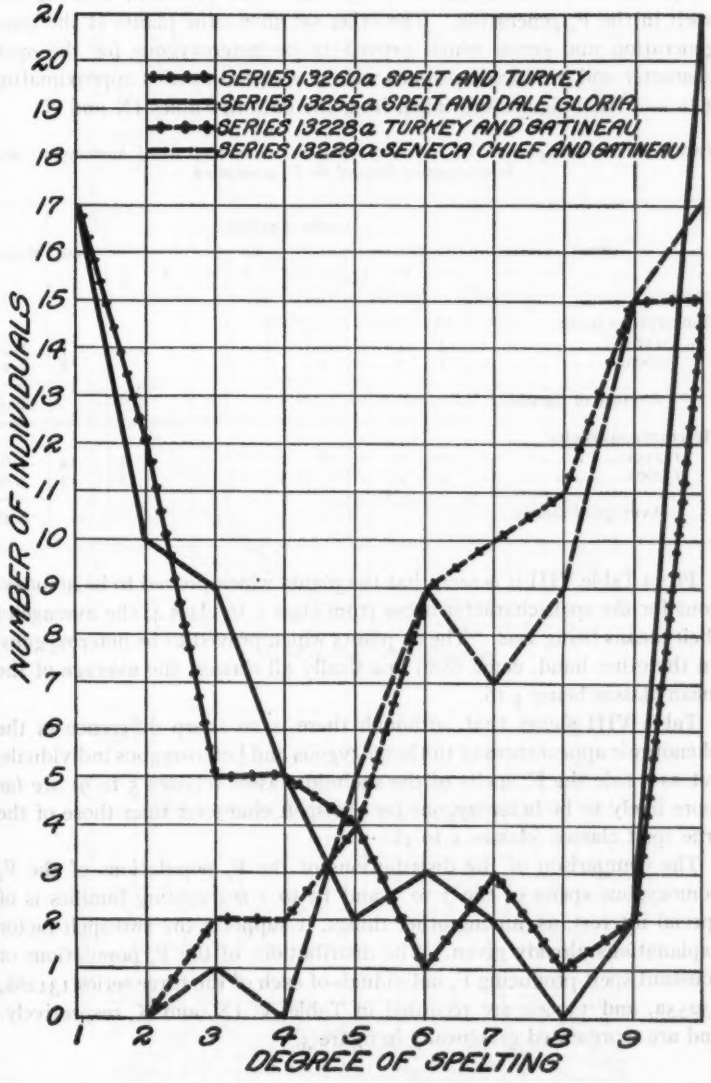
SERIES 13260a SPELT AND TURKEY
SERIES 13255a SPELT AND DALE GLORIA
SERIES 13228a TURKEY AND GATINEAU
SERIES 13229a SENECA CHIEF AND GATINEAU
NUMBER OF INDIVIDUALS
DEGREE OF SPELTING
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
1 2 3 4 5 6 7 8 9

FIG. 2.—Degrees of spelting of F_2 population true spelt × sativum crosses (13255a and 13260a) as compared with the curves of sativum × speltoid crosses (13228a and 13229a) of the same generation.

been prepared to show these differences. Two sets of frequencies are represented. One set represents the classes of spelt inheritance of the F_2 plants of series 13255a and 13260a, which produced nothing but spelt in the F_3 generation. The other set shows the plants of the same generation and series which proved to be heterozygous for the spelt character and produced spelts as well as wheats in ratios approximating 3 to 1. These figures are taken from the data in Tables IX and X.

TABLE VIII.—*Comparison of classes of spelt inheritance of tested homozygous and heterozygous plants of the F_2 generation*

Series.	Grades of spelting.									Totals.	Means.
	1	2	3	4	5	6	7	8	9		
Homozygous spelts:											
13255a	3	3	1	....	....	....	....	....	....	7	1.71
13260a	1	5	1	1	....	....	....	....	....	8	2.25
Average of means	....	....	....	....	....	....	....	....	....	....	1.98
Heterozygous spelts:											
13255a	1	2	2	2	2	1	3	....	1	14	4.64
13260a	4	3	1	....	2	....	1	....	2	13	3.69
Average of means	....	....	....	....	....	....	....	....	....	....	4.16

From Table VIII it is seen that the plants which proved to be homozygous for the spelt character occur from class 1 to class 4, the average of their means being 1.98. The F_2 plants which proved to be heterozygous, on the other hand, came from practically all classes, the average of the mean classes being 4.16.

Table VIII shows that, although there is no sharp difference in the phenotypic appearances of the homozygous and heterozygous individuals, yet as a rule the F_2 spelts of the speltoid classes (classes 5 to 9) are far more likely to be heterozygous for the spelt character than those of the true spelt classes (classes 1 to 4).

The comparison of the distributions of the F_3 populations of the F_2 homozygous spelts of the 3 to 1 and 15 to 1 segregating families is of special interest, as, among other things, it supports the two-spelt-factor explanations already given. The distributions of the F_3 populations of constant spelt-producing F_2 individuals of each of the three series 13126a, 13255a, and 13260a are recorded in Tables V, IX, and X, respectively, and are represented graphically in figure 3.

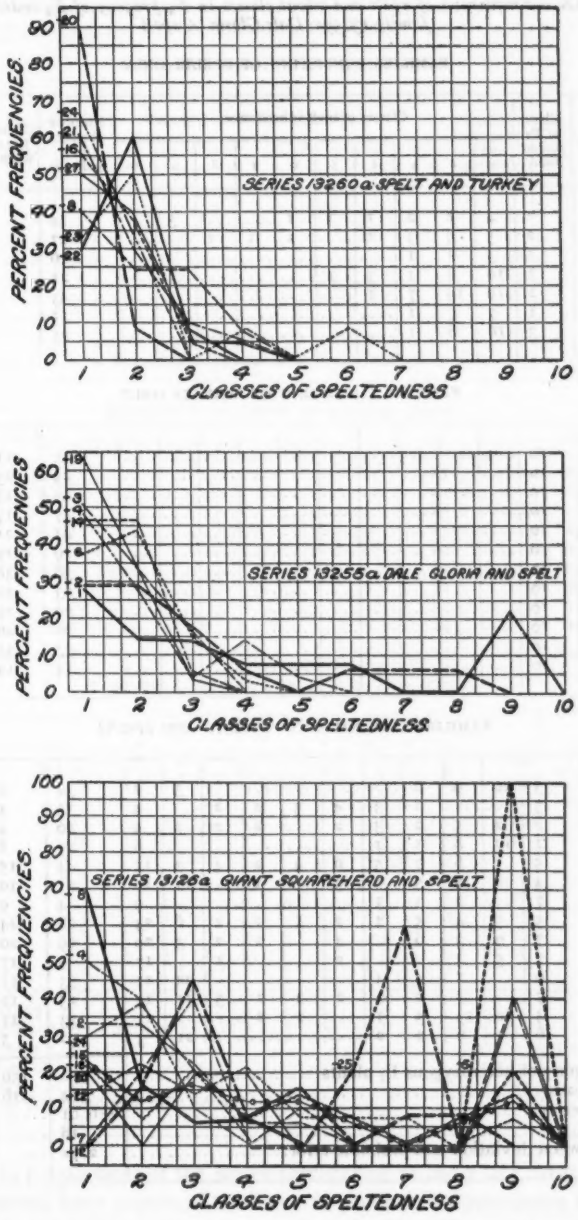
PERCENT FREQUENCIES
SERIES 13260a SPELT AND TURKEY
CLASSES OF SPELTEDNESS
SERIES 13255a DALE GLORIA AND SPELT
CLASSES OF SPELTEDNESS
SERIES 13126a GIANT SQUAREHEAD AND SPELT
CLASSES OF SPELTEDNESS

FIG. 3.—Comparison of F_2 generation curves of the progeny of F_1 spelts which yielded only spelts (series 13260a, 13255a, and 13126a).

TABLE IX.—*Frequencies of spelt and wheat classes in F_3 progeny of F_2 individuals in family 13255a, Dale Gloria × spelt*

FAMILIES CONSISTING OF SPELTS ONLY

Pedigree number F_2.	Class of F_2 parent plant.	Classes of spelt inheritance.										Number of spelts and speltoids.	Number of wheats.	Totals.
		1	2	3	4	5	6	7	8	9	10			
1	2	4	2	2	1	1	1	....	....	3	....	14	.....	14
2	2	5	5	3	1	....	1	1	1	....	....	17	.....	17
3	1	3	2	1	....	....	....	....	....	....	....	6	.....	6
4	1	10	6	1	3	1	....	....	....	....	....	21	.....	21
6	2	16	19	7	1	....	....	....	....	....	....	43	.....	43
14	1	7	7	1	....	....	....	....	....	....	....	15	.....	15
19	3	16	8	1	....	....	....	....	....	....	....	25	.....	25
FAMILIES CONSISTING OF WHEATS ONLY														
5	10	....	....	....	....	....	....	....	....	....	....	11	11	11
9	10	....	....	....	....	....	....	....	....	....	....	25	25	25
12	10	....	....	....	....	....	....	....	....	....	....	13	13	13
13	10	....	....	....	....	....	....	....	....	....	....	17	17	17
18	10	....	....	....	....	....	....	....	....	....	....	21	21	21
20	10	....	....	....	....	....	....	....	....	....	....	19	19	19
22	10	....	....	....	....	....	....	....	....	....	....	38	38	38
27	10	....	....	....	....	....	....	....	....	....	....	23	23	23
29	10	....	....	....	....	....	....	....	....	....	....	29	29	29
31	10	....	....	....	....	....	....	....	....	....	....	20	20	20
32	10	....	....	....	....	....	....	....	....	....	....	33	33	33
33	10	....	....	....	....	....	....	....	....	....	....	14	14	14
FAMILIES CONSISTING OF WHEATS AND SPELTS														
7	3	20	9	2	....	....	....	....	....	3	2	34	2	36
8	3	....	....	1	3	4	3	2	2	....	4	15	4	19
10	2	2	5	2	3	2	....	2	2	2	4	20	4	24
11	1	17	8	1	1	....	....	....	....	....	8	27	8	35
15	5	5	8	7	5	6	4	2	4	3	15	44	15	59
16	4	8	5	5	1	3	....	1	....	....	10	23	10	33
17	7	....	2	1	1	....	....	....	....	....	9	4	9	13
21	5	5	4	5	2	1	1	2	2	6	24	28	24	52
23	7	9	3	6	....	4	....	2	2	3	20	29	20	49
24	2	5	1	....	....	2	....	....	1	....	17	9	17	26
25	9	....	1	4	4	....	....	....	....	24	11	33	11	44
26	7	....	2	2	2	2	2	1	3	11	12	25	12	37
28	4	10	13	5	1	....	2	2	....	....	17	33	17	50
30	6	1	6	2	2	....	....	....	....	21	3	32	3	35
Total progeny of heterozygous F_2 plants												356	156	512
Expectations												384	128	.....
Probable error												±6.61	.....	.....
Deviation												18	.....	.....
Ratio between deviation and probable error												2.72	.....	.....

TABLE X.—*Frequencies of spelt and wheat classes in F_3 progeny of F_2 individuals of series 13260a, spelt × Turkey*

FAMILIES CONSISTING OF SPELTS ONLY

Pedigree number F_3.	Class of F_2 parent plant.	Classes of spelt inheritance (F_3). 1	2	3	4	5	6	7	8	9	10	Number of spelts and speltoids.	Number of wheats.	Total.
8	2	5	3	3	1	....	....	....	....	....	....	12	.....	12
20	2	10	1	....	....	....	....	....	....	....	....	11	.....	11
21	4	12	5	2	1	....	....	....	....	....	....	20	.....	20
22	1	4	8	1	....	....	....	....	....	....	....	13	.....	13
23	2	4	6	....	1	....	1	....	....	....	....	12	.....	12
24	2	2	1	....	....	....	....	....	....	....	....	3	.....	3
27	3	10	8	1	1	....	....	....	....	....	....	20	.....	20
16	3	9	6	1	....	....	....	....	....	....	....	16	.....	16

FAMILIES CONSISTING OF WHEATS ONLY

1	10	....	....	....	....	....	....	....	....	....	....	17	.....	17	17
2	10	....	....	....	....	....	....	....	....	....	....	14	.....	14	14
4	10	....	....	....	....	....	....	....	....	....	....	15	.....	15	15
5	10	....	....	....	....	....	....	....	....	....	....	15	.....	15	15
11	10	....	....	....	....	....	....	....	....	....	....	30	.....	30	30
12	10	....	....	....	....	....	....	....	....	....	....	20	.....	20	20
17	10	....	....	....	....	....	....	....	....	....	....	30	.....	30	30
18	10	....	....	....	....	....	....	....	....	....	....	12	.....	12	12
26	10	....	....	....	....	....	....	....	....	....	....	24	.....	24	24

FAMILIES CONSISTING OF SPELTS AND WHEATS

3	9	....	....	1	....	....	....	1	5	6	10	13	10	23
6	1	11	5	....	....	....	....	....	....	....	....	4	16	4	20
7	1	13	6	1	....	....	....	....	....	....	....	8	20	8	28
9	3	5	3	1	1	....	....	....	....	....	....	7	10	7	17
10	1	10	5	3	....	....	....	....	....	....	....	5	18	5	23
13	2	10	3	....	....	1	....	....	....	3	....	7	17	7	24
14	7	....	....	....	....	....	....	....	3	10	4	13	4	17	
15	5	2	....	2	3	4	1	1	1	2	4	16	4	20	
19	2	9	11	6	....	....	....	....	....	....	....	3	26	3	29
25	2	6	6	1	....	....	....	....	....	....	....	4	13	4	17
28	5	1	1	2	....	2	3	1	1	1	5	12	5	17	
29	1	6	5	3	1	....	....	....	1	....	2	16	2	18	
30	9	....	....	....	1	....	1	2	8	10	8	22	8	30	
Total progeny of heterozygous F_2 plants.		73	45	20	6	7	5	5	19	32	71	212	71	283
Expectations												212.25	70.75	.....
Probable error												±4.91	.....	.....
Deviation												.25	.....	.....
Ratio of deviation to probable error												.05	.....	.....

The F_3 populations of the series segregating in the 3 to 1 ratio (13255a and 13260a) have a general tendency to produce the maximum frequencies at class 1, sometimes at class 2. In only 4 families out of 15 are there individuals in classes above the fourth, 10 individuals in 248 receiving the

higher classification. The few individuals found in these speltoid classes at present may be regarded as exceptions. Their significance will be considered later.

The distributions of the families in the series segregating in the ratio of 15 to 1 (13126a) (Table V) are entirely different. They do not take the general course described above. Some of them have very low frequencies at classes 1 and 2. Families 5, 7, and 12 have no individual in class 1, the population of family 5 being composed of class 9 individuals only. Family 25 produced its spelts in classes 6 to 9, inclusive. Of the 12 families being considered 6 produced class 9 individuals, while among the families segregating in the 3 to 1 ratio there is but one instance (13255a, family 1) where class 9 individuals have been produced.

The explanation of the increased variability of the constant spelt-producing families of series 13126a, as compared with series 13255a and 13260a, will be found in the factorial explanations given for these two groups of crosses.

Families 13255a and 13260a segregated in the simple monohybrid 3 to 1 ratio. By hypothesis, all the spelts producing only spelts are supposed to have the genotypic composition SS.

As to the cross 13126a which segregated in the 15 to 1 ratio, it was shown that there were five constant spelt forms, namely:

$$S_1S_1S_2S_2 \quad S_1S_1S_2s_2 \quad S_1S_1s_2s_2 \quad S_1s_1S_2S_2 \quad s_1s_1S_2S_2$$

Although these forms would keep on producing only spelts, they are not genotypically identical.

The fact that in the families segregating in the 3 to 1 ratio there was only one genotypic spelt form and in the family segregating in the 15 to 1 ratio five such forms were present may account for the increased variability among the pure-breeding spelts of the latter cross.

The F_3 progenies can not be separated into the five theoretical genotypic groups just referred to because, among other things, there is positive evidence that modifiers also are concerned which have the tendency to shift the classes one way or the other. This phase of the subject will next be discussed.

MODIFICATION OF THE DEGREE OF INHERITANCE OF SPELT CHARACTERS, DUE TO THE PRESENCE OF MODIFYING FACTORS

For the consideration of the subject of modifiers the analyses will be confined primarily to the spelt classes (1 to 9, inclusive) of the progeny of the heterozygous F_2 individuals of series 13260a, shown in Table X. This family has been chosen because it represents a simple mode of segregation. Whatever is said about modifiers for this family will be found to apply just as well to the other families.

It has been shown that only one spelt factor was concerned in the cross under consideration. All the F_2 heterozygous plants had the formula

Ss and produced spelts and wheats in the 3 to 1 ratio. If these F_2 heterozygous plants have all the same genotypic constitution with regard to the spelt factor we would expect to see them produce similar F_3 spelt distributions. These distributions obtained experimentally are far from being uniform. For instance, plant 13260a–3 (Table X) produced individuals mainly of classes 8 to 9, and plant 13260a–6 produced its spelts in classes 1 and 2 only. The progeny of 13260a–15, on the other hand, showed no definite grouping, the curve spreading from one extreme to the other.

It may be argued that (1) these variations are insignificant; (2) they may be due to variations in soil and other external conditions; or (3) they are merely nonheritable fluctuations.

These arguments may be answered easily:

1. In the first place, let us take the first two frequencies (classes 1 to 9, inclusive), namely, those of 13260a–3 and 13260a–6 (Table X). The means are 8.00 ± 0.29 and 1.31 ± 0.08. The difference between the two means is 6.69 ± 0.30. This difference, it is seen, is very significant. Similar striking differences will be found when the means of the other distributions are compared.

2. With regard to variations due to soil conditions and external factors, it is only necessary to mention that these plants were grown on the same plot of the experimental field. The pedigree numbers following the family number represent the numbers of the rows in which the progeny of each of the F_2 plants was grown. For instance, the progenies of plants 13260a–28, 29, 30 (at bottom of Table X) were grown in three adjacent rows, yet 13260a–28 was composed of individuals contributing to nearly all classes of spelting, 13260a–29 produced practically all typical spelts, and the progeny of 13260a–30 were nearly all speltoid forms approaching the wheat type. So this second objection may also be dismissed.

3. As to the nonheritability of these variations, the objection may be settled by comparing the F_2 and F_3 generations in terms of the coefficient of heredity. If these variations are nonheritable fluctuations, there should be no correlation between the F_2 and F_3. Putting the statement in the affirmative, if there is a significant correlation in the degree of spelting of parent and offspring of the F_2 and F_3, then it is a direct and indisputable proof that these variations are transmitted to the following generations—that is, they are heritable. The accompanying correlation table (Table XI) has been prepared with a view of determining the validity of this last objection. The x-axis represents the mean classes of the F_3 and the y-axis represents the classes of the F_2 individuals which produced these F_3 forms. In this table are included all the progeny of the heterozygous forms of series 13255a and 13260a in order to have a sufficient number of individuals. The coefficient of heredity as calculated is 0.880 ± 0.029. As this coefficient is over 0.5 and over 10 times its

probable error it may be regarded as being very significant. As there is a significant correlation between these two generations, the variations under consideration are not fluctuations due to external conditions but are hereditary variations.

TABLE XI.—*Correlation table showing the classes of spelt inheritance of F_2 heterozygous plants, with the average degree of spelting of the F_3 progeny of each F_2 plant (series 13255a and 13260a)*

Class of spelting of F_2 parent plants	Classes of spelt inheritance (F_3)								
	1	2	3	4	5	6	7	8	9
1			4	1					
2			1	1	2		1		
3			1		1	1			
4					2				
5						2	2		
6							1		
7						1		2	1
8									
9								1	2

Coefficient of heredity = 0.880 ± 0.029

If there were no interference due to modifiers, the curve of the spelt F_3 progeny of the heterozygous F_2 individuals would follow the spelt curve of the F_2 generation, as both the spelts of the F_2 curve and those of the F_3 curves of heterozygous F_2 individuals consist of SS and Ss spelt plants in the proportion of 1 to 2, respectively.

An examination of the F_3 spelts of heterozygous individuals in Table X shows that the curves of the 13 families vary considerably from the curve of the F_2 generation (Table I, series 13260a), although the curve for the totals is much the same.

Again, if there were no genetic interference, all the F_3 progeny curves produced by heterozygous F_2 plants would be expected to follow more or less the same course. The experimental results exhibit wide differences, as the comparison of the classes of individuals 13260a–3, –6, –7, etc., will readily show.

As the presence of multiple factors is entirely out of question, it being proved in this case that the parents of this cross differ in only one factor for spelting, the following explanation may be given to account for these variations. One or more sets of modifiers furnished by the spelt, by the wheat, or by both parents seem to be present where each set of modifiers was in a homozygous dominant condition in one parent and in the alternative condition or absent in the other parent. These modifiers in the presence of the S factor tend to intensify the spelt character.

An example may be given to illustrate the effect which a modifier may produce in a spelt × wheat cross. The modifier which may cause dilution of spelting may be represented by the factor D and may be assumed to be carried by the wheat parent. (If this factor were contributed by the spelt parent, the latter would have been a dilute spelt, which was not the case in these crosses.) The wheat parent will then be represented by ssDD and the spelt parent by SSdd. The genotypic forms of the successive generations will be as follows:

P_1	SSdd spelt.	×	ssDD wheat.	
F_1	SsDd semidilute spelt.			
F_2	1 SSdd.	2 SSDd.	1 SSDD.	1 ssdd.
	2 Ssdd.	4 SsDd.	2 SsDD.	2 ssDd.
				1 ssDD.
	3 typical spelts.	6 semidilute spelts.	3 dilute spelts.	4 nonspelts.
	12 spelts.			4 wheats.

This represents a ratio of 3 spelts of different grades to 1 wheat.

If we assume that the nature of the modifier were to produce intensification of spelt inheritance in the presence of factor S, which in this case may have been carried either by the spelt or by the wheat, we will have, in the F_2 generation, 3 intense spelts, 6 semi-intense spelts, 3 normal spelts, and 4 wheats.

Some of these spelts (intense, normal, or dilute) will breed true to those conditions; others will produce some or all of these forms in different proportions as expected on the factorial hypothesis. If more than one set of modifiers are present the types and their proportions naturally become rather complex.

If, in the crosses 13255a and 13260a, a diluting modifier has been introduced, we would occasionally expect among the spelts (homozygous or heterozygous) some which are grouped in the dilute speltoid classes. The F_3 population of 13126a–5 and –25 (Table V); 13255a–26 (Table IX); 13260a–3, and –14 (Table X); and a number of others represent such cases. The progeny of 13260a–20, –6, –10 and others may represent spelts carrying some intensifying factor.

In conclusion, it may be said with certainty that besides the S factor in series 13255a and 13260a and the S_1 and S_2 factors in 13126a, modifiers are present which tend to dilute or intensify the spelt character.

In statistical studies of density in wheat, the junior author has found two characters whose mode of inheritance is almost identical with that of the spelt character. When a dense wheat (*T. compactum*) is crossed with a lax wheat (*T. vulgare*) a 3 to 1 segregation is found in the F_2 generation. The F_2 density curve consists of two distinct curves. One of these is a skew curve in the dense classes which contains 75 per cent of the individuals. After a gap, the other curve, which is composed of the lax segregates containing the remaining 25 per cent of the F_2 population, begins. Although the F_3 progeny of these heterozygous dense plants of the F_2 generation invariably produce bimodal curves similar to that of the F_2 just described, their modes or the means of the dense and lax curves shift at times considerably toward the lax classes and sometimes toward the denser classes, much in the same manner as does spelting. A similar phenomenon has been observed by Nilsson-Ehle (*8*) among his dense × lax wheat crosses.

The other parallel case is density of the type just mentioned, but in this case the modifier is known to be the spelt factor itself. The curves of the progeny of the heterozygous dense individuals of dense wheat × spelt crosses have the general bimodal form, but the populations which, in addition to density, carry the S factor always have their density curves shifted toward the lax classes.

With some spelts, the S factor shifts the density curves so much toward the lax classes that this S has to be regarded also as an inhibiting factor for density.

Hull-lessness in oats, according to Love and McRostie (*7*), is inherited in a similar manner. While this character segregates in the simple mendelian ratio of 1 hulled to 2 intermediates to 1 hull-less, the intermediate forms vary appreciably as regards the percentage of hulled kernels they produce. By correlating the percentage of hull-lessness of parent and offspring, they have shown that these variations within the 1 to 2 to 1 ratio are hereditary.

The mode of inheritance of the spelt character as shown in Tables IX and X closely resembles also Castle's (*2*) case of hooded rats, which had for a time aroused considerable controversy for and against the question of inconstancy of unit characters. In numerous crosses between rats having the hooded pattern and the wild (totally pigmented) or the Irish (white belly) types the hooded pattern behaved as a mendelian recessive. The ratio of nonhooded to hooded F_2 offspring was 3 to 1, showing that the hooded condition is dependent upon a single factor difference. Among the hooded individuals a considerable degree of variation was observed with respect to the degree of the extension of this pattern. By making selections for many generations in plus and minus directions

Castle was able to increase and decrease the pigmented area. His belief then was that the variations observed in the race of hooded rats were not mere fluctuations but were hereditary variations in the sense that the factor for the hooded condition had undergone alterations.

The assumption of unit-factor inconstancy, which Castle applied to account for variation of pigmentation of his hooded rats of course can not be applied for the analogous variations in the groupings of the spelt individuals, for, if this were the case, variations in this same extent should have been present among the self-fertilized population from which the parental form was selected. The classes of spelt inheritance in the parental strain ranged from 1 to 4, the mode being between classes 1 and 2. No departures nearly as great as those found in the homozygous extracted spelts of the F_3 generation were observed among this parental population. The study of the F_2 generation shows clearly that either some modifier or modifiers were introduced by the nonspelt parent or were carried by the spelt parent, but these modifiers were reduced to a recessive state as a result of crossing.

PRODUCTION OF SYNTHETIC WHEATS BY CROSSING TWO SPELTS, AND SYNTHETIC SPELTS BY CROSSING TWO WHEATS

The writers frequently have obtained synthetic spelts in interspecific crosses in wheat. No indication has been observed as to the possibilities of producing true wheats in crosses between two different nonwheat species. It is theoretically possible, however, that such forms eventually will be produced in crosses between certain kinds of spelts. This supposition may be explained by taking as an example the results of one of the experiments discussed at length in this paper.

In the case of cross 13126a it was shown in detail that two spelt factors S_1 and S_2 were involved; that the F_2 segregates which bred true to the spelt character were not all genetically identical; and that they were composed of five genotypic forms, namely:

$$S_1S_1S_2S_2 \quad S_1s_1S_2S_2 \quad S_1S_1S_2s_2 \quad S_1S_1s_2s_2 \quad s_1s_1S_2S_2.$$

As long as these forms are allowed to be selfed, as they are in nature, no wheats ever segregate; but, by hypothesis, in a number of crosses between these five forms, a certain proportion of wheats are expected to appear in the following manner:

1. Crosses producing no wheats:

$S_1S_1S_2S_2 \times$ any other genotype; $S_1s_1S_2S_2 \times s_1s_1S_2S_2$; $S_1S_1S_2s_2 \times S_1S_1s_2s_2$.

2. Cross where one out of every four F_1 plants will produce 6¼ per cent wheats:

$S_1S_1S_2s_2 \times S_1s_1S_2S_2$.

3. Crosses where half of the F_1 plants will produce 6¼ per cent wheats:

$S_1S_1s_2s_2 \times S_1S_1S_2S_2$; $S_1S_1S_2s_2 \times s_1s_1S_2s_2$.

4. Cross where all F_1 plants will produce 6¼ per cent wheats:

$S_1S_1s_2s_2 \times s_1s_1S_2S_2$.

If wheats segregate from these crosses it will prove further the correctness of the two-factor hypothesis. It will also lead to the expectation that genotypic forms similar to the above, and other combinations as well, exist among the so-called pure commercial spelt forms and when the proper cross is made among these commercial spelts, a certain number of synthetic wheats may be produced in the F_2 generation.

It is easy to understand how the wheat character, being distinctly hypostatic, may be carried from generation to generation by the spelt type. But how can the spelt type segregate from a wheat × wheat cross? How can one conceive the spelt factor, which is so pronouncedly epistatic to the wheat character, as being carried by a wheat without being manifested phenotypically? The explanation is simple. It was shown that modifiers are involved in these crosses. Common wheats occasionally carry modifiers which tend to dilute the spelt character. Some of these modifiers were shown to be so effective that they grouped all of the spelts in class 9. Most of the class 9 individuals, as recorded in the foregoing tables, resemble wheat so closely that no one would be likely to call them true spelts.

If a certain diluting modifier can shift the spelts to class 9, a group of these may readily shift the spelt to classes between 9 and 10. If these diluting factors are reduced to a homozygous dominant condition, the dilute spelt which will be classified as 10 will breed true to type and be considered as wheat, although from a genetic standpoint such a form is a spelt.

As long as such sorts are allowed to self-fertilize they will produce a so-called pure line consisting of a constant wheat type. Their spelt characteristics are exhibited only when crossed with a common wheat which carries the factor for dilution in a recessive state. In the second generation of this cross the segregates which carry the S factor with the factor for dilution in a recessive state; that is, SS dd, will be spelts.

Fortunately, experimental evidence can be cited to support this statement. One of the writers has observed at the Kansas Agricultural Experiment Station over 20 spelts among F_2 hybrid plants derived from a number of wheat × wheat crosses where one of the parents was a rust-resistant variety of winter wheat and the other was Preston, Marquis, or Haynes Bluestem, well-known varieties of spring wheats. These parental types and some of the spelt segregates are shown in Plate 33, B.[1]

None of the F_1 plants in these crosses were spelts, or at least passed for spelts, although they might have shown some spelt characteristics in a weak form. In the F_2 generation, however, depending upon the cross, the proportions of wheat to spelts varied roughly from 3 to 1 to over

[1] The authors are indebted to Professors John H. Parker and L. E. Melchers for allowing them to photograph these forms and use them in connection with this paper.

100 to 1, with some sets of crosses producing no spelt at all. Besides the true spelts, a number of speltoid forms also segregated.

The absence of the spelt type in the F_1 generation shows that the absence of the spelt character in one of the parents was due to the presence of an inhibitor in the parent plant which carried the S factor. If the appearance of the spelt form in the F_2 generation was due to complementary factors furnished by both parents, the spelt should have appeared in the F_1 generation. Such was not the case.

The cultures consisted of over a thousand F_2 plants. It is not now absolutely necessary to know how, or exactly in what proportion, these appeared. The purpose of citing these examples is to substantiate the views expressed above regarding the possibilities of producing synthetic spelts from wheat × wheat crosses, which might have been regarded as a mere speculation in the absence of this experimental evidence. The fact that there were no spelts grown near the P_1 or F_1 plants and that spelts appeared in more than one cross excludes the possibility of accidental or natural cross-fertilization.

These observations show that common wheats may carry the spelt factor, but the latter can not express itself because one or more diluting or inhibiting factors are carried with it. Some of these diluting factors may be regarded as inhibiting factors which are not totally dominant but produce intermediacy in a heterozygous state.

From the small percentage of spelts which appeared in the F_2 generation in some cases, it may be inferred that there is one and in some cases more diluting factors.[1]

The production of synthetic spelts in wheat × wheat crosses just considered is similar to the synthetic production of *T. dicoccum dicoccoides*, the so-called "Wild Wheat" of Palestine, in the *vulgare* × *durum* cross (*6*). The wild character, consisting of a number of interdependent specific characters, is strongly dominant over both the *sativum* and the *durum* types, as is the spelt type toward *sativum*. Yet in both instances the character showing strong dominance toward either of the parental forms was carried by one of the parents together with a factor inhibiting in one case the wild and in the other case the spelt characters.

MODIFICATIONS OF MENDELIAN RATIOS

The question of modifiers whose presence in the production of the spelt character was demonstrated in various ways brings us to the consideration of the modifications of mendelian ratios. As all spelts or all wheats are not alike with respect to their ability to intensify, repress, or inhibit the production of the spelt characters, it is natural to expect

[1] Nilsson-Ehle (*8, 9*) and Kajanus (*3, 4*) have also observed the occurrence of spelts in certain *sativum* × *sativum* crosses. They support the correctness of the foregoing observations and tend to preclude the assumption of the possibility of the occurrence of some accidental or natural crossing of one of the *sativum* parents with a spelt.

certain modifications of the 3 to 1 ratio. For instance, in certain spelt × wheat crosses, depending upon the potency of the diluting factors, the proportion of wheats to spelts may increase in certain amounts. In some instances, the increase of wheats will be slight, so that the obtained deviation from the 3 to 1 ratio, which will be on the side of excess for the wheat class, will be considered within or near the limits of the probable error and the inheritance will be regarded as simple mendelian. Perhaps series 13255a, where an increased proportion of both constant breeding wheats and F_3 wheat segregates of heterozygous F_2 plants are obtained, represents such a case.

It also is possible that the ratio may fall between 3 to 1 and 1 to 1 in case the diluting factor is very strong. Here, then, will be an excess in the homozygous wheat class at the expense of the homozygous dominant spelt class. If factors of both dilution and of intensification are introduced in the same cross, the experimental ratios will defy any attempt at simple factorial explanations. The writers have obtained a cross where the F_2 generation suggested a possible 3 to 1 segregation, but on examining the F_3 generation, which was composed of a fairly large population, neither the individual segregations nor the totals of these approached in any way 3 to 1 or 1 to 2 to 1 expectations.

It naturally follows from the foregoing discussion that in spelt-wheat crosses wide departures from simple ratios occasionally may be expected.

SUMMARY

T. spelta and *T. sativum* are differentiated by a number of linked specific characters, which are present in one species and absent in the other. These characters, so far as observed, are not inherited independently but are transmitted as a group.

In crosses between a spelt and common wheats the F_1 hybrid shows dominance of the spelt, but this character appears in a somewhat diluted form. In the second generation all classes of spelt inheritance are obtained. In order to classify these forms, 10 arbitrary classes were erected, class 1 representing the true spelt and class 10 the total absence of this character. The intermediate classes represent different grades of spelt inheritance.

In most of the material studied there was but one factor difference for spelt, but in two cases two spelt factors were present. Both 3 to 1 and 15 to 1 ratios were obtained. These ratios were verified after determining the genotypic constitution of the F_2 plants, which gave pure breeding spelts, inconstant spelts, and pure breeding wheats in the ratios of 1 to 2 to 1 and 7 to 8 to 1, respectively. Of the constant spelts produced in crosses with this latter ratio, approximately half yielded (in the F_3 generation) spelts and wheats in the ratio of 15 to 1 and the other half in the ratio of 3 to 1, as expected on the two factor hypothesis.

The speltoid form "Gatineau" when crossed with wheats gave also a 3 to 1 segregation of spelts and wheats, but the curves showing the classes of spelts produced by this cross were entirely different from the curves produced by the spelt-wheat crosses which segregated in the same ratio.

Aside from the factor or factors for spelting, there is positive evidence showing the presence of intensifying and diluting modifiers which tend to affect the degree of spelt characters without affecting to any extent the ratios of spelts to wheat. Some of the diluting modifiers tend to act as inhibitors.

The progeny of all heterozygous spelts of the Ss type do not produce a similar spelt curve. There are wide discrepancies in the spelt inheritance of the progeny of these forms. These variations within the spelt classes have been found to be hereditary and to be caused by modifiers.

The theoretical possibility of producing synthetic wheats in crosses between certain pure-breeding spelts is shown.

Experimental evidence also is presented showing that, in spite of the fact that the spelt character is dominant over the wheat form, the former may be synthetically produced by crossing certain wheats, provided one of the wheats carries a spelt factor together with an inhibitor and that the other wheat carries neither.

It is shown that, if intensifying, inhibiting, and diluting modifiers are introduced in a cross, wide departures may be expected from the 3 to 1 and 15 to 1 ratios.

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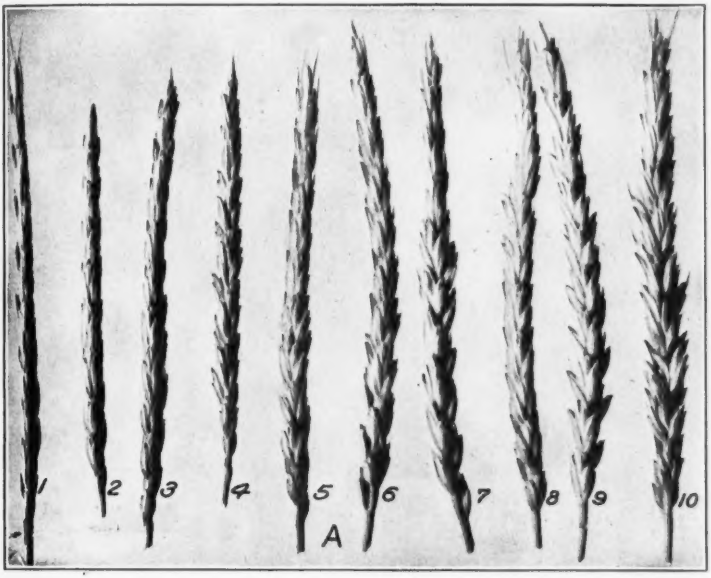
PLATE 33

A.—Wheat spikes showing different degrees of spelting. 1 and 2 are intense spelts; 3 to 9 are intermediate forms, showing varying degrees of dilution of the spelt character; 10 is a pure-breeding wheat (*sativum*) form, showing no trace of spelting. The numbers represent approximately the types falling in the 10 classes of spelting.

B.—Snythetic spelts produced in F_2 generation in wheat × wheat crosses; a, b, c, and d are the *sativum* parent plants; b–1 spelt form of the progeny of a × b; c–1 to c–5 spelt forms of the progeny of a × c; d–1 and d–2 spelt forms of the progeny a × d.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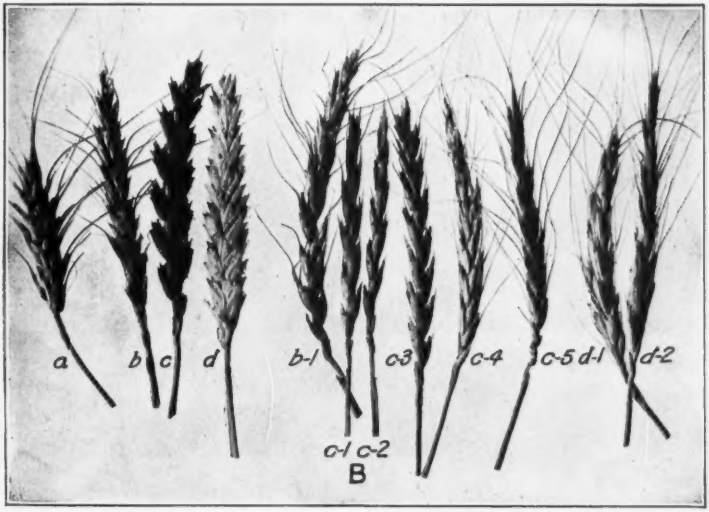
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b
c
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b-1
c-1
c-2
c-3
c-4
c-5
d-1
d-2
B

PLUM BLOTCH, A DISEASE OF THE JAPANESE PLUM, CAUSED BY PHYLLOSTICTA CONGESTA HEALD AND WOLF [1]

By JOHN W. ROBERTS, *Pathologist, Fruit Disease Investigations, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

In June, 1905, W. M. Scott of the Bureau of Plant Industry, United States Department of Agriculture, collected near Fort Valley, Ga., fruits of the Japanese plum (*Prunus triflora* Roxbg.) affected with a disease very closely resembling the apple blotch, due to *Phyllosticta solitaria* E. and E. In the diseased areas were spore-bearing pycnidia which were found also on the leaves in gray papery spots resembling those on apple leaves caused by *Phyllosticta solitaria*. On May 27, 1908, the disease was again observed by Scott on both fruit and foliage of the Burbank plum at Montezuma, Ga. It was found to be rather common in several orchards about Montezuma, in some cases causing enough damage to injure seriously the market value of the fruit. In one orchard a large part of the fruit was affected, and many specimens bore from 15 to 20 spots each.

On May 29, 1917, the writer collected near the same locality Japanese plum fruits and leaves affected with the same disease. In the single orchard in which the disease was found, most of the fruit was heavily nfected and rendered nearly worthless. Considerable difficulty was encountered in finding the disease again, as the Japanese plum industry in Georgia had about passed out. Lack of demand for the fruit coupled with the susceptibility of all parts of the tree to various diseases and insect pests had caused growers either to eradicate their trees or to let them die. At present there are almost no Japanese plum orchards remaining in Georgia, and all of the trees in which plum blotch was found have been eradicated. So far as the writer knows, then, the disease no longer exists, though it is to be looked for throughout the South as far west as Texas. Should the growing of Japanese varieties of the plum be revived in the South, blotch may prove to be one of its most serious diseases, as it is very destructive, and probably would be exceedingly difficult to control.

The varieties found to be affected were Abundance, Burbank, and what was apparently an unnamed seedling.

[1] A brief description of this disease was published as an abstract of a paper presented at the Ninth Annual Meeting of the American Phytopathological Society. (ROBERTS, John W. PLUM BLOTCH. (Abstract.) In Phytopathology, v. 8, no. 2, p. 74. 1918.)

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DESCRIPTION OF THE DISEASE

The infected parts on the unripe fruit appear as dark-colored raised areas with fringed margins and are somewhat roughened by the presence of small blisters and depressions (Pl. 34, B). As in the case of apple blotch, the skin often becomes ruptured as the fruit increases in size.

On the ripe fruit the blotched parts appear as irregular browned areas 3 to 6 mm. in diameter and consist of an aggregation of from 4 to 20 sunken spots, each separate spot being 1 mm. or less in diameter. At this stage the spots have a peculiar light blue cast owing to the "bloom" of the ripe plum covering the browned epidermis. The diseased area is rather superficial, extending only slightly below the epidermis. The affected tissues become hardened and somewhat leathery and show no tendency to decay.

Small, glistening pycnidia are produced in considerable numbers even in the younger spots. Quite commonly there are 25 to 30 scattered promiscuously about in each blotched area. Infection evidently takes place when the fruits are very young, since the spots found May 29 were well formed and bore pycnidia with mature spores. Judging from the writer's inoculation experiments, infection probably took place five to six weeks earlier, or about the middle of April.

On account of its characteristic appearance on the fruit, the disease has been given the common name of "plum blotch."

On the upper surface of the leaf blades (Pl. 34, A), the spots are angular, rather small (about 0.5 mm. across), brown when young, but later becoming gray or silvery in color. They may be numerous, as many as 200 sometimes appearing on a single leaf. Usually only a single pycnidium is present in each spot, except where two or more spots have coalesced to form a single large spot. Affected areas are also found on the petioles and on the veins of the lower surface, especially on the midrib. On these the diseased areas are much larger than on the upper surface of the blade and are black and sunken. Pycnidia, bearing spores, are present in great abundance.

Pycnidia, apparently identical with those found on the fruit and leaves, were found also in small light-colored, often slightly sunken areas on the twigs; but, as spores were lacking, positive identification could not be made. It is possible that these pycnidia had discharged their spores early in the spring and had brought about the early infections on the fruit.

CAUSE OF PLUM BLOTCH

By comparison with type specimens, the organism involved in the production of plum blotch has been found to be identical with the fungus described by Heald and Wolf [1] as *Phyllosticta congesta*. Heald and

[1] Heald, F. D., and Wolf, F. A. New species of Texas fungi. *In* Mycologia v. 3, no. 1, p. 8. 1911.

Wolf found the fungus on the leaves only of *Prunus* sp. in Texas Their description is as follows:

Maculis minutis, .5–.8 mm diam., brunneis numerosis, venis limitatis; pycnidiis solitariis in quaque area, 50–125 μ diam.; sporulis globulosis vel leniter elongatis, hyalinis 6–9 μ.

On Prunus sp. Boerne (Texas) 1554 (Type).

On the upper surface of the leaf are very numerous brown areolae bounded by the veins of the leaf. The lower surface may not be discolored. These minute spots fuse, and each contains at its center a single black pycnidium. The pycnidia contain globular or slightly oval, clear spores.

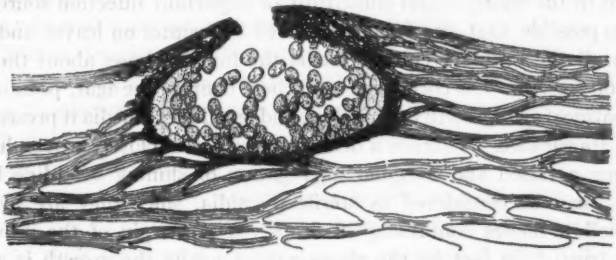


FIG. 1.—Section through a pycnidium of *Phyllosticta congesta*, showing spores. Natural infection on plum fruit, Georgia 1917. × 340.

Heald and Wolf do not mention the fact that the older spots become gray or silvery, though the type specimens as well as those collected by Scott and the writer show this to be the case. The spots on these leaves and those on Georgia specimens collected by the writer show a marked resemblance, and the fungi found upon them are morphologically the same. The spots on the leaves collected by the writer have a greater tendency to fall out.

The pycnidia (fig. 1) are glistening, lens-shaped, erumpent, on the leaves 65 to 120 μ in diameter, on the fruit 60 to 120 μ in diameter. On the average, pycnidia on the fruit are somewhat larger than those on the leaves. Spores on the leaves measured 7 to 9 μ in diameter, on the fruit 8 to 9 μ. Spores from younger spots were invested with gelatinous envelops which were sometimes lengthened into appendages (fig. 2). Spores from older spots do not show these envelops, and they are not to be found in the dried herbarium specimens. The young spores of *Phyllosticta solitaria* have such an envelop. In fact, *P. solitaria* and *P. congesta* resemble one another so closely that on purely morphological grounds they might be considered as identical. Since the ascogenous stage of neither fungus is known, the writer prefers to retain the name *P. congesta* as a matter of convenience, unless it is shown by cross inoculations that the fungus on the apple and that on the plum are identical in every way.

FIG. 2.—Spores of *Phyllosticta congesta*, with the gelatinous envelops which are sometimes present. From pycnidia on plum fruit, Georgia 1917. × 680.

Of course the final test of identity would lie in whether or not the ascogenous stages of the two fungi, assuming them to exist, would prove to be identical.

Specimens of *Phyllostica congesta* on fruit and foliage of *Prunus triflora* have been deposited in the Pathological Herbarium, Bureau of Plant Industry, United States Department of Agriculture.

It is not known how the fungus is carried over from one season to another. If it occurs on the twigs, as the writer is inclined to think, there would be good reason for believing that production of spores from twig lesions in the spring would constitute an important infection source. It is also possible that the fungus survives the winter on leaves and fruit.

On all the ordinary culture media the fungus shows about the same type of growth. On corn meal agar, beef agar, prune agar, potato agar, and oatmeal agar growth is very slow, and on all these media it presents the same appearance. There is a dense black mass of closely woven hyphae forming a raised and irregular aggregation of shining bead-like bodies which may be considered as sterile pycnidia, since they are more or less hollow bodies containing oil drops. The margin of the growth is often fringed; in fact on the above-named media the growth is almost as blotch-like as it is on the fruit of the plum. On sterilized stems of Melilotus the growth resembles that on the agars, but spores are often formed though very scantily.

On Japanese plum twigs growth is also very slow. Pycnidia and spores are formed in about two months. Pycnidia are formed on the bark and may also be formed at the cut end of the twig, in which case they are densely aggregated.

Sterilized apple twigs proved to be the best medium for the production of spores, though two to three months must elapse before spore production begins. On this medium the only sign of growth by the fungus is the formation of a dense mass of hyphae and pycnidia, closely aggregated at the upper end or at an abraided place on the side of the twig. On all the media used the type of growth exhibited by *Phyllosticta congesta* differs somewhat from that of *P. solitaria*. On sterile apple twigs, for instance, the latter produces pycnidia which are scattered over the bark, whereas the pycnidia of the former are formed only at the cut ends of the twigs.

In 1917 the fungus was isolated from both fruit and leaves by the poured plate method, using spores, and by planting bits of the diseased tissues in plates.

In the spring of 1918, no spores had been obtained in cultures, but inoculations were made by spraying the young fruits and leaves of Abundance and Burbank plums with bits of hyphae and sterile pycnidia suspended in sterile distilled water. The results were negative in every case.

In 1919, spores obtained from apple twig cultures and suspended in sterile distilled water were applied to fruit, foliage, and twig of Abundance plums on May 15. Where cultures originally obtained from plum fruits were used, two fruits were found with two typical blotches on each of them; three leaves were found with scattering spots, each spot typical of the disease and each bearing a single pycnidium with the characteristic spores of *Phyllosticta congesta*. Like results were obtained by the use of cultures obtained from the leaves; one fruit showed three typical blotches with pycnidia and two others showed one; seven leaves were successfully infected. From all these artificially inoculated parts, the fungus was reisolated and proved to be *P. congesta*.

No lesions were found on the twigs.

Inoculations made upon Japanese plums with spores from pure cultures of *Phyllosticta solitaria* gave negative results in 1918, 1919, and 1920, though the spores were applied to fruit, foliage, and twigs at frequent intervals throughout the spring.

Though the inoculation experiments herein reported upon are sufficient to prove *Phyllosticta congesta* the cause of plum blotch on leaves and fruit and show the fungus on the fruit to be identical with that on the leaves, they are not as complete as the writer should wish. All the inoculation work was done at Arlington, Va., under conditions probably unfavorable to the fungus, since it has been found naturally only in regions much farther south.

It is planned to carry on further inoculation work with both the plum blotch and apple blotch Phyllostictas. The writer expects eventually to obtain successful inoculations on plum twigs using *Phyllosticta congesta* as inoculum.

CONTROL MEASURES

No attempts to control plum blotch have been made. One would expect that control might be had by spraying with a strong fungicide at intervals beginning shortly after the petals have been shed as is the case with apple blotch. Dilute lime-sulphur solution and Bordeaux mixture injure Japanese varieties of the plum so severely as to preclude their use during the growing season. It is also doubtful whether or not dilute lime-sulphur solution would control severe cases of disease, since it will control only mild cases of apple blotch. Self-boiled lime-sulphur can be used with safety on the Japanese plum, but it is a fungicide which is even weaker than dilute lime-sulphur solution. It seems probable, therefore, that should this disease ever become an important one, its control will present a problem of considerable difficulty, though it is realized that the reasoning by analogy in which the writer has just indulged may easily lead to wrong conclusions.

SUMMARY

Plum blotch, a hitherto unknown disease of the Japanese plum (*Prunus triflora*), has been found in Georgia. In addition to the fruit, the leaves and possibly the twigs are affected. The lesions on fruit and leaves greatly resemble those of the apple caused by *Phyllosticta solitaria* E. and E.

Varieties Abundance and Burbank were found to be susceptible. An unnamed seedling, probably also belonging to *Prunus triflora* was found to be severely infected.

From diseased fruits and leaves the fungus, *Phyllosticta congesta* Heald and Wolf, was isolated and grown in pure culture. Spores obtained from cultures on sterile apple twigs when suspended in distilled water and sprayed on healthy fruits and leaves produced characteristic lesions of the disease.

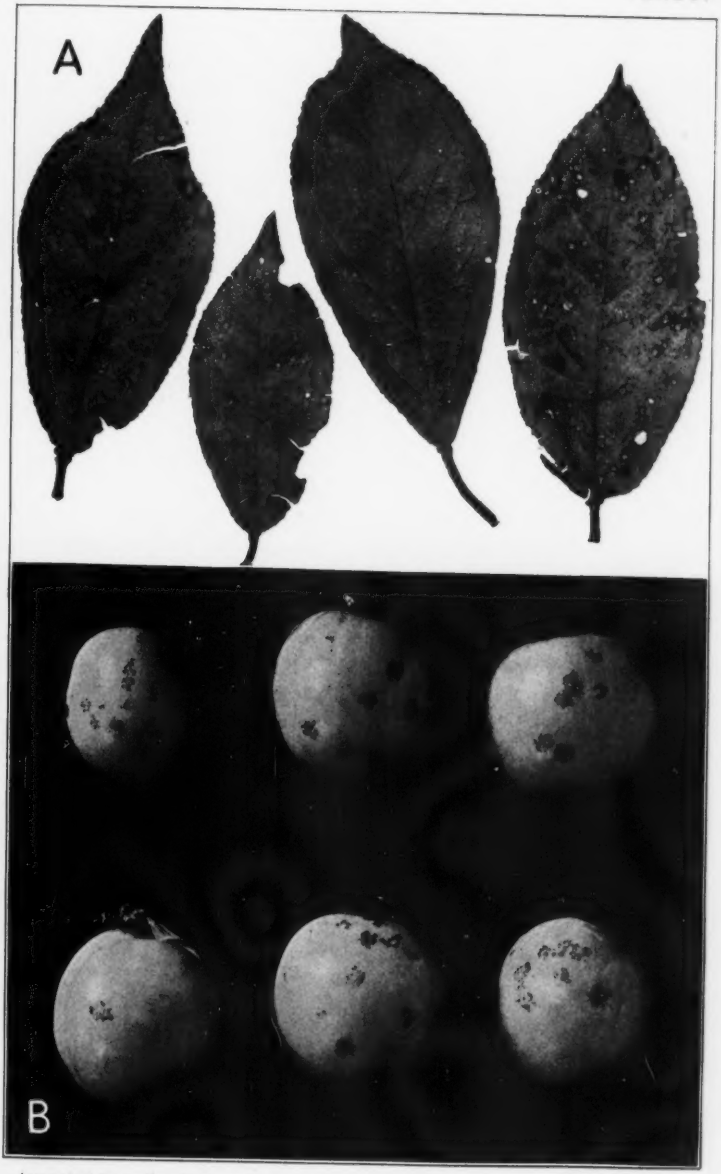
Phyllosticta congesta Heald and Wolf is to be considered for the present as different from *P. solitaria* E. and E., though greatly resembling it. Inoculation experiments on plums using spores from pure cultures of *P. solitaria* were negative.

No attempts have been made to control plum blotch, but the possibilities of control are discussed.

PLATE 34

A.—Plum leaves affected with *Phyllosticta congesta*, Georgia, 1917.

B.—Plum fruits affected with *Phyllosticta congesta*, showing the characteristic "blotches," Georgia, 1917.


A
B

A COMPARISON OF THE PECTINASE PRODUCED BY DIFFERENT SPECIES OF RHIZOPUS

By L. L. Harter, *Pathologist*, and J. L. Weimer, *Pathologist, Office of Cotton, Truck, and Forage Crop Disease Investigations, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

Recent investigations by Harter and Weimer [1] showed that *Rhizopus tritici* Saito, an organism demonstrated to be parasitic on sweet potatoes, produces a powerful intracellular and extracellular pectinase which dissolves the middle lamella so that the cells readily separate without themselves undergoing any noticeable alteration. A suspension of 0.25 gm. of the enzym powder in 25 cc. of water was found to completely macerate sweet potato disks 1 mm. in thickness in two to five hours. Furthermore, the solution on which the fungus grew was even richer in pectinase, maceration of the sweet potato disks being completed in one to three hours.

Since the foregoing results have been published Harter, Weimer, and Lauritzen [2] have concluded experiments which showed that out of 11 species of Rhizopus studied 9 were parasitic on the sweet potato. Furthermore, these investigators found that the species differed in degree of parasitism, both as regards the percentage of infection and the rapidity of decay.

The present investigations, therefore, had for their object to determine (1) if pectinase is produced by all species of Rhizopus and, if so, to what extent and (2) if its production is any indication of the parasitism of the species.

TECHNIC

The methods employed in carrying out macerating experiments with the different species of Rhizopus were for the most part the same as those used in previous work to which reference [1] has already been made, although some slight modifications were necessary to meet certain phases of the problem. Three sets of experiments were carried out with each organism. All the species were included in a single experiment and the macerating action was determined for all at the same time, so that the results for each species are directly comparable for a single experiment. The culture medium was so prepared and in sufficient quantity as to make

[1] Harter, L. L., and Weimer, J. L. Studies in the physiology of parasitism with special reference to the secretion of pectinase by Rhizopus tritici Saito. *In* Jour. Agr. Research, v. 21, no. 9, p. 609-625. 1921. Literature cited, p. 624-625.

[2] Harter, L. L., Weimer, J. L., and Lauritzen, J. I. The susceptibility of the different varieties of sweet potatoes to decay by Rhizopus nigricans and Rhizopus tritici. *In* Phytopathology, v. 11. 1921. In press.

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it uniform in all the flasks for all organisms. Four flasks (2 liters), containing 300 cc. of the culture medium, were inoculated with each one of the species in each experiment, and the cultures were incubated for three days.

The macerating action was determined for the following species of Rhizopus: *chinensis* Saito, *nodosus* Namysl, *tritici* Saito, *maydis* Bruderl, *delemar* (Boid) Wehmer and Hanzawa, *arrhizus* Fischer, *oryzae* Went and Pr. Geerligs, *nigricans* Ehrnb., *reflexus* Bainier, *artocarpi* Racib., and *microsporus* v. Tieg.

It has been shown [1] that the different species of Rhizopus do not all have the same optimum temperture for growth. Some species thrive at high temperatures, some at relatively low temperatures, and others at a temperature intermediate between the two extremes. Therefore, the 11 species studied have been separated into three groups with respect to their temperature relations. In all the experiments connected with the present investigations the same grouping of the different species has been observed, thus subjecting each organism to as nearly the optimum temperature for its growth as possible.

The cultures of *chinensis* were incubated at 40° C., those of *nodosus*, *tritici*, *maydis*, *delemar*, *arrhizus*, and *oryzae* at 30°, and those of *nigricans*, *reflexus*, *artocarpi*, and *microsporus* at 20°. Although so far as temperature is concerned the results are not strictly comparable, preliminary experiments showed that more reliable data could be obtained by growing the different organisms at temperatures suited to their growth than by subjecting them all to a uniform temperature. Some of the species, as for example *nigricans*, which requires a relatively low temperature, make no growth or only a feeble growth at 30° and none at 35°. On the other hand, *chinensis*, a high temperature form, makes a reduced growth at 30° and a feeble growth at 20°.

At the close of the incubation period (three days) the mycelial growth was lifted from the culture flask and the substrate was filtered through a fine grade of muslin. The mycelium was treated subsequently by acetone and ether according to the method previously described.[2] The solutions from the different flasks in which the same species had grown were made into a compound sample thoroughly shaken, and 25-cc. portions were used for maceration experiments. Likewise all the fungous felts of the same organism grown in the different flasks were brought together and treated as one sample, a weighed portion of the dried mycelium being used for maceration of the raw disks. Two types of controls were run with each set of experiments, as follows: (1) Sweet-potato decoction on which the fungus had grown for three days, which after the removal of the mycelium was steamed for 15 minutes to inactivate the enzym; (2) decoction which was identical with that used for

[1] HARTER, L. L., WEIMER, J. L., and LAURITZEN, J. I. op. cit.
[2] HARTER, L. L., and WEIMER, J. L. op cit.

inoculation purposes but which had not supported a fungous growth. Maceration by the enzym in the solution and in the mycelium was carried out at a temperature of 40° C. for all the species. Before the addition of the raw sweet-potato disks the solutions and suspensions of the mycelium were held for one hour at 40° in order to bring them to the temperature at which maceration was to take place.

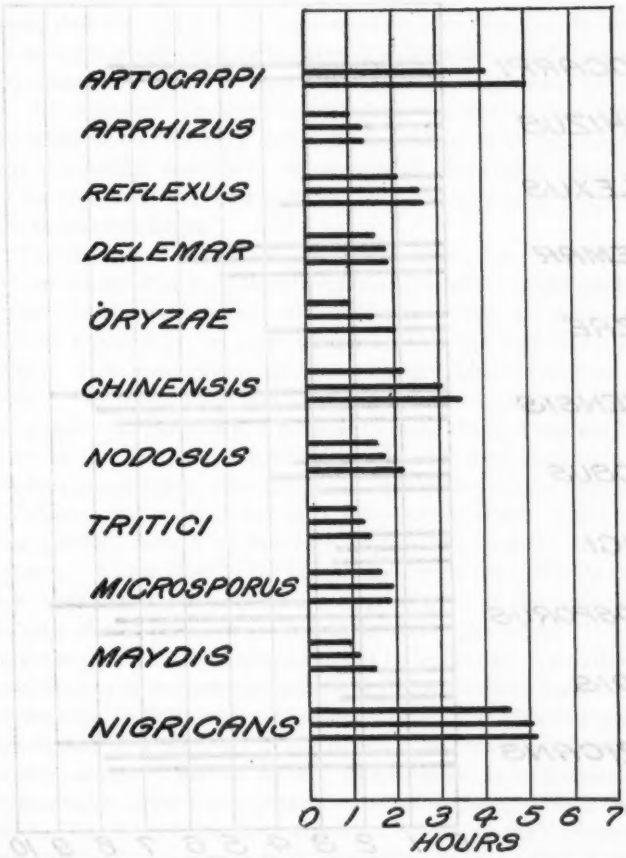

FIG. 1.—Graph showing the time required by the different Rhizopus species to completely macerate sweet-potato disks by the enzym in the solution on which the fungi had grown for three days; also the comparative rate of maceration in the three experiments.

Maceration with the mycelium was carried out by the use of 0.5 gm. ground in sand and suspended in 25 cc. of water. All the sweet potato disks (1 mm. thick and 1.5 cm. in diameter) required for maceration in the solution on which the fungus grew and in a water suspension of the mycelium were cut from a single potato for an entire experiment of all the species.

EXPERIMENTAL DATA

The results obtained in the different experiments both as regards the maceration in the solutions and in a water suspension of the mycelium are represented graphically in figures 1 and 2. Each of the vertical lines of a single group represents the results obtained for a particular organism in a single experiment. The length of the vertical lines indicates the

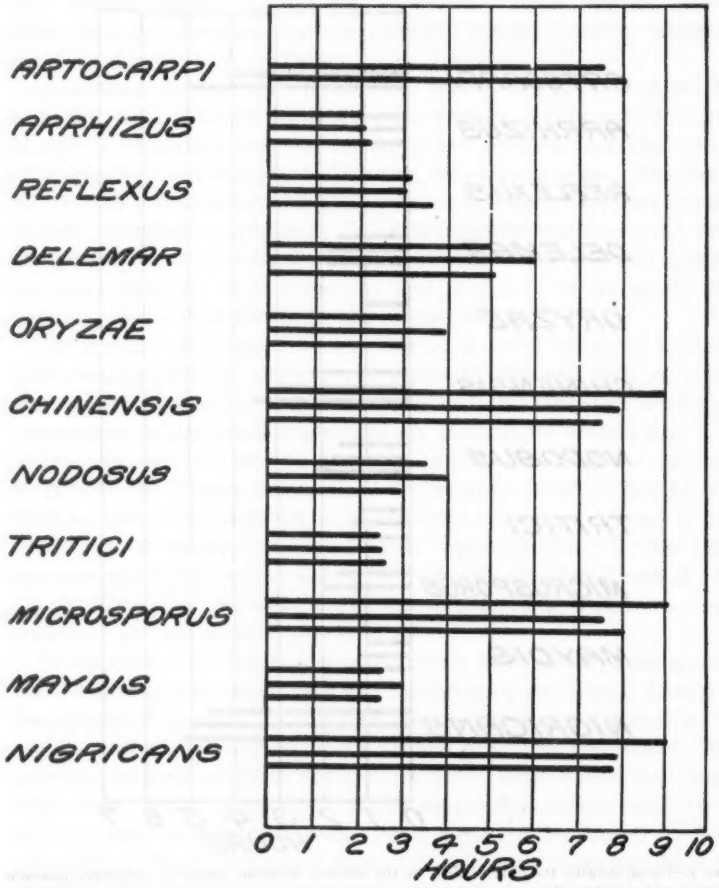

FIG. 2.—Graph showing the time required by the different Rhizopus species to completely macerate sweet-potato disks by the enzym contained in ½ gr. of the mycelium; also the comparative rate of maceration in the three experiments.

length of time in hours required to complete maceration of the disks, 1 cm. being equivalent to one hour. From these figures a direct comparison can be made of the results obtained from the different species as well as the variation in the results of the same species in different experiments.

DISCUSSION OF RESULTS

VARIATION

A comparison of the results as shown by figures 1 and 2 indicates that under the conditions of these experiments maceration was completed by the enzym exuded into the solution in a shorter length of time than by that contained in the mycelium. This difference, however, does not mean that the enzym is more powerful or more abundant in the solution than in the mycelium since no attempt was made to employ an amount of mycelium that would be equivalent in macerating power to the enzym of the solution. In these experiments maceration was regarded as complete when the disks pulled from opposite sides separated without any perceptible resistance. In completely macerated tissue coherence of the cells is entirely lost and the tissue can be readily pulped between the thumb and finger.

The data show that a considerable amount of variation exists in the results obtained in the different experiments with a single species both in respect to the solution and the mycelium. There are probably several factors responsible for these variations. In the first place a different supply of the sweet-potato decoction was prepared for each set of experiments. In spite of the fact that the different solutions were prepared to be alike as nearly as it is possible to make them, it can not be said, in view of the fact that different potatoes were used each time, that the various preparations were identical. After the cultures were inoculated incubation was carried out at a temperature which varied very little but possibly enough to influence slightly the rapidity and volume of growth. At the close of the incubation period the substrate and mycelium were handled as nearly alike as possible in all the experiments, but in spite of such precautions some variations might result. It would seem that the greatest source of error might be attributed to a variation in the composition of the potatoes from which the raw disks were cut. In this connection preliminary experiments showed that different potatoes are macerated in a different length of time the variations, however, being within relatively narrow limits. Furthermore, it is probable that the composition of the sweet potato is gradually changing with the increase in the length of time after digging. So far as their susceptibility to maceration is concerned it is interesting to note that a comparison between newly dug potatoes and those stored for several months showed that the latter are macerated in a shorter time than the former. Although the present experiments were carried out with a single variety the various experiments were conducted in sequence so that the later experiments were made on what might be termed older potatoes.

COMPARISON OF SPECIES

MACERATION OF DISKS IN THE SOLUTIONS

It appears from figure 1 that two species, *nigricans* and *artocarpi*, macerate raw sweet potato disks more slowly than any of the others, followed by *chinensis* and *reflexus* in the order mentioned. The other species complete maceration in a relatively short time, the most rapid being *arrhizus*, *tritici*, and *maydis*.

MACERATION OF DISKS IN A SUSPENSION OF MYCELIUM

With respect to maceration by the mycelial enzym, four species, *nigricans*, *microsporus*, *chinensis*, and *artocarpi*, stand out as being conspicuously slow. So far as the mycelium is concerned *delemar*, a species intermediate between the slow and rapid forms, is less active than *reflexus* but more active than the latter when the solutions are used. Likewise the enzym contained in the mycelium of *microsporus* macerates slowly, while that in the solution, on the other hand, disintegrates the tissue rapidly. *Chinensis* shows a similar relationship existing between the enzym of the mycelium and that of the solution, although this species does not stand out as conspicuously as *microsporus*.

From the few illustrations cited it is evident that there is no complete correlation between the activity of the mycelial enzym and the activity of that exuded into the substrate. An examination of figures 1 and 2 shows that the different species do not secrete an equivalent amount of pectinase, since the completion of maceration by the enzym of both the mycelium and solution may vary greatly. It is conceivable and the results of these investigations seem to indicate that some species give up their enzym to the solution more readily than others. For example, the solution on which *microsporus* grew is relatively rich in pectinase while the enzym contained in the mycelium acts slowly. *Delemar* is another outstanding example of the same phenomenon.

PECTINASE PRODUCTION IN RELATION TO PARASITISM

If a relationship between the production of pectinase by the different species of Rhizopus and their parasitism could be shown to exist, considerable light might be thrown on the physiology of parasitism, especially among fungi which are characterized by their ability to dissolve the middle lamella in advance of their growth. In a previous publication [1] it was pointed out that all the species of Rhizopus studied were parasitic on sweet potatoes with the exception of *microsporus* and *chinensis*. These two species were studied in connection with the others. They were given equal opportunity to cause decay, but in no case was there any evidence to indicate parasitism. However, both of these

[1] HARTER, L. L., WEIMER, J. L., and LAURITZEN, J. I. op. cit.

species produced pectinase. The amount of pectinase in the mycelium at the end of the growth period was relatively small, but *microsporus* and to a lesser degree, *chinensis*, exuded enough into the culture solution to cause maceration in a much shorter time than either *nigricans* or *artocarpi*, both of which are parasites. Maceration of sweet-potato disks by means of the mycelial enzym of the two parasitic and nonparasitic species just mentioned was completed in about the same length of time. *Nigricans* is the most commonly isolated species and is probably responsible for most of the loss to sweet potatoes caused by this group of fungi. At a suitable temperature it decays sweet potatoes and other vegetables rapidly. The middle lamellae of sweet potatoes decayed by this species are dissolved some distance in advance of the growth of the mycelium, so that coherence is lost. In the early stages, at least, the cells themselves are not invaded by the fungus. The same may be said of *artocarpi*. However, in cultures *nigricans* and *artocarpi*, in contrast to the other species, exude a very small amount of enzym into the substrate and retain very little in the mycelium. *Delemar*, a species which readily decays sweet potatoes, seems to give up most of its pectinase to the substrate, so that maceration by means of the mycelium is relatively slow, at least within the limits of these experiments. All the other species are vigorous parasites, decaying the sweet potato within a few days under favorable conditions. They also produced large quantities of pectinase, relatively speaking, some of which is exuded into the solution and some retained by the mycelium, as shown by the fact that maceration, by both the mycelium and solution, is comparatively rapid.

SUMMARY

(1) The secretion of pectinase by 11 species of Rhizopus has been studied. All the species were found to produce pectinase and to exude some of it into the culture solution.

(2) The amount of pectinase produced varies with the species, grown under identical conditions. The mycelium of four species—*nigricans*, *microsporus*, *chinensis*, and *artocarpi*—and the solution on which two—*nigricans*, and *artiocarpi*—are grown is comparatively weak in pectinase. *Chinensis* and *microsporus*, whose mycelial enzym is weak, secrete it abundantly into the substrate.

(3) Two species, *nigricans* and *artocarpi*, both of which are parasitic on the sweet potato, secrete a relatively small amount of pectinase. On the other hand, *chinensis* and *microsporus*, two nonparasitic species, while retaining a small amount of enzym in the mycelium, secrete a comparatively large quantity of enzym into the culture solution.

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